

BULLETINS
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MARINE ECOLOGY
(FORMERLY HULL BULLETINS OF MARINE ECOLOGY)

VOLUME IV

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LIST OF PERSONNEL OF THE OCEANOGRAPHIC LABORATORY EDINBURGH 1951-1959

Officer-in-Charge :

K. M. Rae, O.B.E., B.Sc., Ph.D.(London), 1935-1957.

(Dr. Rae was Officer-in-Charge from 1950 to 1957, when he was appointed Professor of Biological Oceanography in the Agricultural and Mechanical College of Texas.)

R. S. GLOVER, B.Sc.(Manchester), 1945-

(Mr. Glover was appointed Officer-in-Charge in August, 1957.)

Research Biologists :

G. T. D. HENDERSON, D.S.C., B.Sc., Ph.D.(Bristol), 1931-

C. B. Rees, D.Sc.(Wales), 1937-1956.

(Dr. Rees died on 2 September, 1956.)

B. M. Bary, M.Sc., Ph.D.(New Zealand), 1957-1959.

M. H. WILLIAMSON, M.A., D.Phil.(Oxon.), 1958-

F. R. Vane, M.Sc.(Liverpool), 1947-1958.

G. A. ROBINSON, M.A.(Cantab.), 1951-

D. A. Priest, B.Sc.(London), 1952-1953.

D. H. Mills, B.Sc.(London), 1954-1956.

J. M. COLEBROOK, B.Sc.(London), 1956-

V. BAINBRIDGE, B.Sc.(Dunelm.), 1959-

Experimental Officers :

Miss D. E. JOHN, 1947-

Miss M. F. Jobson, B.Sc.(St. Andrews), 1947-1954.

G. A. COOPER, 1947-

W. W. BROWN, B.Sc.(Leeds), 1948-

D. C. T. FORSYTH, B.Sc.(Aberdeen), 1954-

Miss B. I. BARNES, B.Sc.(London), 1954-

Names in italics indicate those members who have left the laboratory.

The dates after each name indicate the years of service in the Oceanographic Laboratory and in the Department of Oceanography at the University College of Hull.

EXPLANATION

A non-technical account of the contents of Volume IV

by G. T. D. Henderson, D.S.C., B.Sc., Ph.D.

WHEN *The Hull Bulletins of Marine Ecology* were first published, it was decided to preface each volume with a brief non-technical account of its contents.

The Hull Bulletins of Marine Ecology, volumes I, II and III, comprising Nos. 1 to 24, were published by the University College of Hull, to present the results of the College's Department of Oceanography. In April, 1950, the programme of research of this Department was transferred to the Scottish Marine Biological Association, and the staff moved to Edinburgh where the new Oceanographic Laboratory was opened on 31 October, 1952 (see *Explanation*, Vol. III).

This volume IV is the first to be completed under the title of *Bulletins of Marine Ecology*, but it is a continuation of the *Hull Bulletins of Marine Ecology* and the serial numbering of the individual papers continues from the earlier series.

Bulletin No. 25. The first paper in this volume is a report by Mr. K. M. Rae on the progress of the Continuous Plankton Recorder Survey, giving details of the records obtained in 1950, 1951 and 1952, with charts showing their distribution. The scope of the Survey was similar to that in the earlier years when the headquarters of the laboratory were in Hull; the object being to obtain, each month, plankton records along thirteen routes, seven traversing the North Sea, five running into the Atlantic, and one north from Bergen into the Norwegian Sea. There was a steady increase in the total mileage sampled, from about 35,000 miles in 1950 to 37,000 miles in 1951, and to 40,000 miles in 1952. Mr. Rae makes a special acknowledgment of our debt of gratitude to the owners, masters and crews of the participating vessels, and to the other personnel of the companies and organizations concerned; without their generous and unfailing cooperation the continuation of the work would not be possible.

Bulletin No. 26. The Plankton Indicators, devised by Professor Sir Alister Hardy for investigations of the planktonic environment of the herring, have been subjected to much modification and development since the Standard Indicator and the Miniature Indicator were described in 1936. In this paper Mr. R. S. Glover describes and illustrates the various types which have been developed for use from

fishing vessels and research ships. The original models of the Indicator sampled at only one depth and the plankton was collected on a flat disc of silk so that fishermen could easily see the sample and compare it with photographs of typical discs. From this design Mr. Glover has developed a model which can be used to sample simultaneously at a number of different depths; for some purposes of research it is convenient to increase the size of the catch by fitting a small net in place of the flat disc of silk. The towing characteristics of the various models are described, and the sampling efficiency is discussed in relation to the earlier report by Dr. H. Barnes in Volume II, No. 16.

Bulletin No. 27. Nearly all the bottom-living animals, which form the food of the trawl-caught fish, have larval stages which are found in the plankton. These larvae may themselves provide food for young fish and for plankton-eaters such as the herring. The larval forms in the Plankton Recorder material were the subject of a special study by Dr. C. B. Rees, whose death in 1956 was a serious loss to the Edinburgh Laboratory and to marine biology in general; he had been a member of the Recorder team since 1937.¹ Dr. Rees began his study of the larvae by establishing a new technique for identifying the young stages of the bivalve (lamelli-branch) molluscs, and by describing their distribution in the North Sea in 1949 (see Volume III, Nos. 19 and 20).

In this *Bulletin No. 27*, based on the material collected in 1950 and 1951, he clarified the identification of more of these larvae and discussed the distribution and fluctuations in abundance of the common species. In a special consideration of the common mussel (*Mytilus edulis*) he explained the possible origins of the stocks of larvae and the ways in which they may become distributed, by water movements, in the North Sea. He suggested that the pattern so defined might be associated with the "paths" of the inflowing Atlantic water, and showed that variations in this pattern could be associated with changes in the observed distribution of the copepod *Metridia lucens*, which is an indicator of a mixture of Atlantic and North Sea waters.

Bulletins Nos. 28 and 29. In these papers Dr. Rees continued his accounts of the distributions of the pelagic young stages of bottom-living forms taken in the Recorder Survey. The greatest concentrations of the echinoderm larvae (i.e. of the starfishes and allied forms) were found in the Heligoland Bight, where the maximum numbers occurred in June and July. Further north, off the Firth of Forth, the greatest numbers were more often found in April and May. Detailed distributions of the commonest species are shown, and differences between the dominant kinds in the northern and southern halves of the North Sea are demonstrated. Although some agreement was observed between the numbers of larvae

¹ Obituary notices were published in *Nature* (Vol. 178, p. 672), *Journal du Conseil International pour l'Exploration de la Mer* (Vol. 22, p. 267) and in the *Annual Report for 1956-57 of the Scottish Marine Biological Association* (p. 3).

occurring in the plankton and the distribution of the adults as shown by bottom surveys, there did not appear to be a simple correlation between them. From a comparison between the distributions of the larvae of Echinoderms and those of the common mussel, Dr. Rees suggested that the distribution of both groups of larvae might be influenced by a common factor. The main features of the distributions and seasonal fluctuations of the Polychaete, Cyphonautes and Cirripede larvae are outlined briefly.

In *Bulletin No. 29* Dr. Rees returned to the study of the decapod larvae which he started in volume III, No. 22. In the period 1947 to 1951 the largest catches of all species were taken in the months July to September, the year 1949 being the most productive in this period and 1947 the year of least abundance. Even so, the level reached in 1949 was well below that attained in 1938. The specific composition of the catches showed that different species appeared to be dominant in different years. Such fluctuations in the apparent success of various species in different years was not confined to the decapod larvae; similar differences were found among the lamellibranch and echinoderm larvae, and in some of the permanent plankton forms. The annual fluctuations in abundance of the six commonest species are illustrated and their percentage contributions to the totals caught in 1947 to 1951 are shown. Finally, a comparison between the distributions in the four "quarters" of the North Sea of decapod, lamellibranch and echinoderm larvae suggests that the main spawning concentrations of these three groups do not coincide.

Bulletin No. 30. Mr. K. M. Rae reports on the Continuous Plankton Recorder Survey with a list of records and charts for 1953 and 1954. The basis of the survey was unchanged but alterations in the duties of the Ocean Weather Ships permitted an extension of sampling further westwards into the Atlantic, south of Iceland. The addition of a Faroese ship, M.S. *Tjaldur* provided a most useful route from the Norwegian coast, *via* the Shetlands, to the Faroe Islands.

Bulletin No. 31. Dr. D. I. Williamson of the Port Erin Laboratory gives an account of a survey in the Irish Sea area carried out with the standard Plankton Indicator in 1951 and 1952. The Continuous Plankton Recorder has never been used in the Irish Sea, but comparable sampling was achieved by taking successive tows with the standard Indicator from the research vessel *William Herdman* over standard routes. Sampling was confined to daylight hours but this was not thought to have affected the assessment of the abundance of various forms, although it might account for the absence of adult euphausiids in the catches.

In spite of the currents entering the Irish Sea from both north and south, the majority of the oceanic species which have been associated with the penetration of Atlantic water into other European waters have seldom been recorded from the Irish Sea. It is thought, therefore, that the transport of Atlantic water may be too limited and too slow for these species to get into the Irish Sea proper, even if occa-

sional occurrences are recorded from the marginal zones. In normal years only *Nyctiphanes couchii* and *Centropages typicus* appear to behave as indicators of water entering the Irish Sea, although *Meganyctiphanes norvegica*, *Sagitta elegans* and *Metridia lucens* (usually considered as indicators of some admixture of Atlantic water in the Channel and North Sea) appear to be resident in the Irish Sea. The distributions of the other species regularly found in the area are discussed, and the fluctuations in their abundance are associated with the available information on the circulation of the waters of the Irish Sea and the variations in this caused by changes in the inflow of water from both north and south.

Bulletin No. 32. One of the types of Plankton Indicator described by Mr. Glover in *Bulletin No. 26* has been used since 1947 in an investigation of the plankton ecology of the north east Scottish Herring Fishery. The use of the Indicator by commercial vessels has meant that the methods of sampling were dependent on fishing habits and this resulted in practically all the samples being obtained just before nightfall; these were augmented by other samples taken at all times of the day and night from research ships. It seemed necessary, therefore, to determine whether charts of plankton distribution could be constructed from such a combination of daylight and night-time sampling. Mr. Glover and Mr. J. A. Pope (of the Marine Laboratory, Aberdeen) report in this paper on a statistical treatment of catches obtained using the Plankton Indicator by day and by night, with the twofold objective of determining whether diurnal vertical migrations of plankton animals were affecting the sampling of commercial vessels, and if so, whether any differences between day and night samples were constant or not. It is shown that for the copepods, and particularly for *Calanus*, there were significant differences between night catches and day catches. These differences, however, were not constant; they tended to be greatest around midsummer and least in early and late summer. Usually the catches were greater by night but, in the spring and autumn, the differences were slight, or even reversed. The explanation of these results is discussed in relation to the findings of other workers that (i) diurnal vertical migrations are probably maximal in midsummer, and (ii) the upper population of copepods probably retreats from the surface during the summer. It was not possible to determine a correction constant which could be used to equate samples taken by night with those taken by day but it is emphasized that the diurnal differences which were found were not large in relation to the overall seasonal or spatial differences which occur in the plankton community.

Bulletin No. 33. The late Dr. Rees, in Volume II, No. 14, described the differences between the two forms of the copepod *Calanus finmarchicus*. His work was based on material then available from the Recorder Survey and it has been modified by the discovery in 1953 of an intermediate form. Mr. J. Mauchline, while a student assistant at the Aberdeen Laboratory of the Scottish Home Department, has contributed this paper in which an attempt is made to separate the

various forms by statistical methods. He has made an appreciable contribution to the knowledge of the morphology of *Calanus*, but has not been able to define simple measurement criteria by which the two forms and any intermediate individuals may be separated with certainty.

Bulletin No. 34. In 1924 Professor Sir Alister Hardy began to study the relationships between the herring and its planktonic environment; this work was continued from 1930 to 1933, and was resumed in 1947, when a more detailed survey of the north eastern Scottish herring fishery was commenced from Fraserburgh. Much work has been done in this area, and is still continuing. This first report by Mr. Glover, Mr. G. A. Cooper and Mr. W. W. Brown sets out the background to the fishery which must be understood as a prelude to the study of the problems of the catches and the environment, the plankton of the area, and the shoaling and feeding habits of the herring. This work was made possible through the voluntary assistance of drift-net fishermen who collected all the samples of plankton and provided detailed information about their night-by-night fishing. No praise could be too high for the assistance which was received from more than a hundred skippers and their crews. The authors' first consideration is to assess the reliability of the fishing fleet as a mechanism for sampling the stocks of fish, and its efficiency for this purpose. This is essential, as the methods used in this work were determined by the behaviour and practices of fishermen gaining their living, and not by the application of specially designed sampling techniques. For example, continuity of sampling of both herring and plankton was always broken at the week-ends, as there is no fishing on Saturday or Sunday nights.

This very comprehensive study of the operation of the fishery from Fraserburgh shows that the fleet usually worked on the inshore edge of the natural population of herrings. The more distant grounds, even when more profitable in terms of catch, were neglected while nearer areas could provide a sufficient, although smaller, return. The Fraserburgh (and Peterhead) vessels found their best fishing progressively further south in each successive year from 1947 to 1954, suggesting a re-distribution of the stock of fish during this period. The exploration of the area followed the same sequence each year, the fishing being concentrated first over the near shallow banks, then over deeper water, and finally further southwards and shorewards towards the spawning areas. These three phases may reflect stages in the distribution and migration of different components of the herring stock.

An examination of the methods of searching for and exploiting the shoals of fish showed that most of the fleet concentrated on the position of a previous high catch, fishing there for two or perhaps three nights, then moving on to another such position which had been determined by a vessel working independently, often well away from the main body; the fleet appeared to work in a manner which ensured continued contact with the shoals. The aggregation of vessels on to the fish was more marked in the later part of the season when the fish were preparing

to spawn than in the earlier part of the year when the fish were feeding actively. This may be a reflection of differences in shoaling behaviour at different stages of the herring's annual cycle.

When comparisons between skippers were made, it appeared that successful men fished alone more often than the less successful who preferred to fish among a concentration of boats. But all solitary fishing was not necessarily successful, the average catch in areas with moderate numbers of boats being higher than that in areas with few. It is presumed that among the solitary searching skippers there were some who were consistently skilful at picking the right area; these men were important in helping the fleet to keep in contact with the most profitable shoals of fish.

Bulletin No. 35. In earlier reports on the young fish in Volume II, No. 15 and Volume III, No. 24 the main emphasis lay on the general distributions of groups of species, with special attention to the fluctuations in numbers noted from year to year. In this paper Dr. G. T. D. Henderson shows the detailed distribution in the Atlantic of the young planktonic stages of the Blue Whiting (*Gadus poutassou*); they were only found in late March, April and May of each year, with a peak of abundance in the second half of April. The young stages taken with the Plankton Recorder were found in the same area in every year: to the west of the Hebrides and over deep water just outside the Continental Slope. The young have been very numerous in some years, suggesting that considerable stocks of this medium sized gadoid fish may be available should it be necessary to exploit them. The material included the smallest stages at a hatching size of 2.75 mm. and drawings and descriptions of these help to fill a gap in the knowledge of the life history. A preliminary note on the rate of growth in the first few months of life is included.

Bulletin No. 36. The precise recognition of different forms or varieties of a species may often be of particular importance in the study of its distribution. In this paper Mr. G. A. Robinson describes and discusses the two forms of the diatom *Rhizosolenia alata* (Brightwell), of which the larger, var. *indica* (Ostenfeld), has an oceanic distribution, seldom extending into the shallower waters of the Continental Shelf, whereas the smaller, var. *alata* (Brightwell), is found in both oceanic and coastal waters. The distinction between these two depends on the size of the cell and Mr Robinson has used size frequency measurements, together with studies of the change in cell size at certain periods of the life history, to work out the differences between the two forms.

Bulletin No. 37. The importance of the copepod *Calanus* in the food chain in the sea has long been recognised, and its direct relationship with the feeding of herring has been the subject of extensive research. The Recorder Survey has provided a great collection of material for studies of its distribution in the North Sea and the north-eastern Atlantic; in this account, published posthumously, the

late Dr. C. B. Rees described and discussed the distribution of *Calanus finmarchicus* (Gunn) in its two forms 'finmarchicus' and 'helgolandicus'.

In the oceanic waters of the Atlantic the abundance of *Calanus* increased from south to north and reached a maximum off the Norwegian coast as shown by results from the Recorder route from Bergen to the Arctic. The Atlantic to the north of Rockall yielded very few samples containing the 'helgolandicus' form, but south of Rockall 'finmarchicus' was rarely taken except in the spring. In the North Sea *Calanus* was most abundant in the central area; the two main areas for 'helgolandicus' were (i) over the Great Fisher Bank and the eastern side of the Dogger Bank, and (ii) the Skagerrak and the Danish coast, but late stages of this form were much more abundant north of Ireland than anywhere in the North Sea.

Over the whole area studied the largest numbers of young stages occurred in the spring months, but smaller peak numbers were sometimes noted in the summer, especially over the Great Fisher Bank; these were generally precursors of concentrations of 'helgolandicus'. In the north western part of the North Sea the main concentrations of late stages occurred in the autumn, and were usually 'finmarchicus'. In the central North Sea the main concentration of 'finmarchicus' occurred in May in 1946-48 and 1950-52, but in 1938-39 and in 1953 there were two concentrations, the first in April/May, and the main and larger one in early July. It is thought that these reflect the occurrence of one and of two spring generations respectively.

The seasonal succession of 'finmarchicus' was fairly similar throughout the entire region of the survey, but for 'helgolandicus' the main period of reproduction occurred in spring in the Atlantic and in summer in the North Sea. The questions of the transport of stocks from one area to another, and the effects of the inflow of Atlantic water in to the North Sea are discussed in relation to the distributions found in the various years.

Detailed studies of the structure of closely related plankton forms such as these help to determine the extent to which apparently different types constitute biologically different populations. This is important in analysing the nature of fluctuations; the problem is similar to that of the fishery biologist in defining the limits of separate stocks of herrings and the extent to which such stocks may inter-mingle or, perhaps, even inter-breed.

Bulletin No. 38. The relationship between prevailing winds and the distributions of the young of food fishes have been examined by many workers, and some most interesting associations have been suggested. In this paper Mr. Rae has observed a contemporary correlation between wind along the Leith to Skagerrak recorder route and the distribution of *Metridia lucens* in the northern North Sea in the late autumn and winter of each year. He shows that the apparent easterly displacement of the distribution of this copepod can be correlated with the mean residual wind along the route sampled for the months of November, December and January.

When the same functions of wind are compared with the relative brood strengths, in different years, of the haddock in the northern North Sea it is seen that better recruitment occurred in the years when the wind averaged less than 250 miles per day, no good broods occurring in years when the wind was greater than this. Mr. Rae suggests that the association of the distribution of *Metridia lucens* with the same wind factors which are followed by these good brood years for haddock may be a reflection of the wind conditions required to set up an appropriate mixing of incoming Atlantic water : one which persists for a sufficient time over the haddock spawning areas to provide favourable conditions for spawning, hatching and survival of the young. Mr. Rae's work leaves some further questions to be answered, but part of the value of this kind of analysis is that it may lead to the evolution of forecasting techniques ; for example, if this suggestion is confirmed, knowledge of wind conditions might permit a forecast of the strength of recruitment to a fishery two or three years later.

CONTINUOUS PLANKTON RECORDS:

LIST OF RECORDS, 1950-53.

BY

K. M. RAE, O.B.E., B.Sc.

THE Continuous Plankton Recorder Survey was started from the University College of Hull, in 1931. Previous station lists or summaries of records have been published in the 'Hull Bulletins of Marine Ecology': that for 1931-37 in Vol. I, No. 2; that for 1938-39 in Vol. II, No. 7; and that for 1946-49 in Vol. III, No. 21. The survey was suspended during the war years.

In March, 1950, the responsibility for the survey passed from University College, Hull, to the Scottish Marine Biological Association, and the staff and equipment involved were moved to Edinburgh. The scope of the programme, however, remained as before; the object being to obtain regularly, each month when possible, plankton records along some thirteen routes, seven traversing the North Sea, five running into the Atlantic, and one north from Bergen into the Norwegian Sea. There has been a steady increase in the total mileage sampled, from about 35,000 miles in 1950 to 37,000 miles in 1951, and to 40,000 miles in 1952. It is fitting, therefore, that we should again express our debt of gratitude to the owners, masters and crews of the following vessels, and also to the other personnel of the companies and organizations concerned; without their generous and unflinching co-operation the continuation of the work would not be possible.

S.S. "Harrogate"	}	Associated Humber Lines Ltd.
S.S. "Melrose Abbey"		
S.S. "Gothland"	}	James Currie & Co. Ltd.
S.S. "Horsa"		
S.S. "Borodino"	}	Ellerman's Wilson Line Ltd.
S.S. "Leo"		
S.S. "Spero"		

S.S. "St. Clair"—The North of Scotland and Orkney and Shetland Steam Navigation Co. Ltd.

S.S. "Sarpfoss"—Thor Thoresen & Co. Ltd.

O.W.S. "Weather Explorer"	} Weather Ships Service, Air Ministry, London.
O.W.S. "Weather Observer"	
O.W.S. "Weather Recorder"	
O.W.S. "Weather Watcher"	

O.W.S. "Polarfront I"—The Norwegian Committee on Weather Station M, Oslo.

O.W.S. "Cumulus"	} The Royal Netherlands Meteorological Institute.
O.W.S. "Cirrus"	

The arrangement of this summary of records is just the same as that for 1946-49, presented in 'Hull Bulletin' III, 21. Table I comprises a list of serial numbers and code letters of the records which are arranged in chronological order month by month. The date or dates on which each tow was taken are given together with the *ratio*, or the total mileage towed divided by the number of 2-in. divisions of silk which wound through the machine. This ratio has a significance in the method of estimating the plankton. The filtering silk is cut up into units equivalent to 10 miles of tow, and a constant proportion of this unit is examined under the microscope as a sub-sample of the whole area of silk over which the plankton is spread. The factor used to raise the sub-sample to the total is based on a ratio of 5 miles per 2-in. division of silk, so ratios above or below 5 may make the estimate of the total low or high respectively (see Rae, 1952, p. 154).

Figs. 1 to 6 provide a series of charts, each representing a single month. Any individual record can be found on the chart of the month on which it was taken by its code letter and serial number. On these charts are shown for each record the route steamed by the towing vessel, the direction of tow, and the parts of the record which were taken during the hours of daylight and darkness. Here and there it has been necessary to displace records on the charts, and in these cases arrows indicate the correct position of shooting and hauling.

On occasions extra tows were taken, in addition to the routine monthly series, for the purpose of testing new machines or for obtaining extra data. Usually plankton caught on these records was not fully analysed and consequently they are not illustrated on the charts. The fact that an extra record was taken, however, is noted on the chart by its serial number, thus "+ 88A" and corresponding entry is marked with an *asterisk* in the table.

TABLE I.—*A List of the Records shown in Plates I-VI Arranged by Months.*

The serial number and code letter of each Record is followed by the date or dates on which the tow was taken. The Records marked with an *asterisk* were taken for some special purpose and were in addition to the normal survey: the plankton caught on them has not been fully analysed. The final figure in each entry gives the ratio of miles per division, *i.e.*, the total mileage towed divided by the number of 2-in. divisions of silk that crossed the water tunnel (see p. 2).

1950			1950 (contd.)			1950 (contd.)		
Record.	Date.	Ratio.	Record.	Date.	Ratio.	Record.	Date.	Ratio.
<i>January</i>			<i>April (contd.)</i>			<i>July (contd.)</i>		
158R	1	5.6	37X	15/17	5.1	86K	7/9	5.6
139C	4/5	5.2	36W	15/17	5.5	41X	8/9	6.8
79K	6/8	5.6	144C	18/20	5.1	6J	8/9	4.7
32M	9	5.4	13T	30/1	6.7	37M	12	5.5
32W	20/22	6.0				165B	14/15	4.8
80A	21/22	4.7	<i>May</i>			40W	17/19	5.3
160R	22	5.1	37W	4/6	5.0	26G	17/18	4.7
140C	25/26	5.8	38X	4/5	6.5	90A	22/23	4.6
10T	28/29	5.7	163R	7	4.7	165R	23	4.5
			145C	10/11	5.3	42X	27/28	6.7
<i>February</i>			163B	11/12	4.0	16T	31/1	5.7
33W	8/11	8.2	83K	13/14	5.2			
34X	8/11	7.6	84A	13/14	4.6	<i>August</i>		
81A	11/12	4.8	3J	25/26	4.9	166B	4	5.0
141C	15/16	4.2	84K*	26/28	4.6	41W	9/11	4.8
80K	18/19	5.6	38W	27/29	5.0	38M	12	5.4
161R	26	5.3	39X	27/28	6.2	91A*	12/13	5.0
11T	26/28	6.4	85A*	27/28	5.0	30V	13/15	7.9
			14T	31/1	6.7	27G	15/16	4.7
<i>March</i>			<i>June</i>			87K	18/20	5.6
34W	4/5	6.8	146C	31/1	4.7	43X	19/21	6.8
142C	7/9	5.3	25G	3	4.9	92A	19/20	4.9
82A	11/12	4.8	35M	6	5.1	147C	19/20	5.0
33M	12/13	5.4	85K	9/11	6.3	166R	20	4.6
81K	18/19	5.8	39W	15/17	4.7	17T	30/31	5.7
162R	19	6.0	40X	15/17	6.5			
36X	23/25	4.9	87A	17/18	4.9	<i>September</i>		
35W	23/24	5.4	36M	17/18	4.8	167B	1	4.9
34M	26/27	4.9	4J	17/19	5.1	93A	2/3	4.8
143C	29/30	5.0	164R	18	4.5	44X	8/10	5.8
12T	30/1	6.6	88A*	24/25	5.4	42W	8/10	5.7
			15T	29/30	5.8	28G	13/14	5.2
<i>April</i>						88K	15/17	5.8
162B	7	4.2	<i>July</i>			148C	16/17	5.3
83A	11/12	4.4	89A*	1/2	5.0	31V	18/20	4.4
1J	13/15	4.9	5J	6/8	7.1	167R	23/24	5.8
82K	15/16	5.2						

TABLE I.—(contd.)

1950 (contd.)			1951 (contd.)			1951 (contd.)		
Record.	Date.	Ratio.	Record.	Date.	Ratio.	Record.	Date.	Ratio.
<i>October</i>			<i>February</i>			<i>June (cont.)</i>		
43W	30/1	6.5	51X	3/4	4.8	174R	10	4.2
45X	1/2	5.5	49W	3/4	4.0	174B	11	5.1
18T	1/2	5.7	34G	10/11	4.0	35G	13/14	4.2
29G	10/11	4.2	171B	16/17	4.5	39V	25/26	4.5
168B	13	5.3	94K	16/18	4.6	57X	28/30	5.0
89K	13/15	7.0	96A	20/21	4.9	11J	28/30	4.5
168R	15	4.1	52X	21/23	5.4	23T	30/1	5.1
32V	16/17	4.4	50W	21/23	5.6			
44W	19/21	5.3	172R	25	4.8	<i>July</i>		
46X	19/21	6.9	20T	27/1	5.7	53W	30/1	5.6
149C	22/23	5.3				36G	11/12	4.9
			<i>March</i>			100A	14/15	5.4
<i>November</i>			95K	16/19	4.6	157C	21/22	4.9
30G	7	4.7	51W	17/19	5.2	12J	21/23	4.5
150C	11/12	5.0	97A	17/18	4.7	175B	21/22	4.9
45W	11/13	6.3	172B	17/18	5.4	175R	22	4.4
47X	12/14	5.7	53X	19/21	4.8	58X	24/25	4.6
31G	18/19	4.4	36V	27/29	5.4	99K	27/29	5.5
91K	19/20	5.5				24T	30/31	6.3
33V	21/23	5.3	<i>April</i>			40V	30/1	4.6
169R	26	4.1	7J	5/6	3.9			
19T	28/30	6.4	96K	13/15	4.9	<i>August</i>		
			98A	14/15	5.0	13J	9/11	4.5
<i>December</i>			173B	14/15	5.6	59X	11/13	5.2
46W	1/3	4.9	39M	15/16	5.2	54W	11/13	4.8
48X	1/3	5.8	37V	22/24	4.7	40M	17/18	4.7
92K	9/10	5.0	154C	22/23	5.5	100K	17/19	5.2
151C	9/10	5.2	173R	29	4.4	158C	18/19	5.5
47W	21/22	5.1				176B	18/19	4.9
169B	23/24	4.2	<i>May</i>			176R	19	4.2
94A	26/27	5.8	21T	1/2	4.8	41V	27/29	4.7
			155C	12/13	4.5	55W	30/1	4.4
<i>1951</i>			97K	12/14	5.2	25T	31/1	5.3
<i>January</i>			9J	17/19	4.3			
32G	5	3.3	56X	18/19	6.9	<i>September</i>		
152C	6/7	5.1	38V	28/30	4.7	101A	1/2	5.4
1H	9/10	4.5	22T	30/1	5.1	14J	1/3	4.6
48W	9/11	4.6				60X	1/2	3.6
50X	9/10	4.9	<i>June</i>			37G	3/4	4.5
33G	14/15	5.0	99A	2/3	5.3	101K	7/9	5.0
170B	18/19	4.4	52W	7/9	5.5	177B	16/17	4.8
93K	20/21	5.1	98K	8/10	5.1	15J	20/21	4.6
95A	20/21	4.5	156C	9/10	4.9	56W	22/24	4.4
35V	23/24	4.7	10J	9/11	4.6	177R	23	4.4
171R	23/24	4.2				26T	30/1	5.5

TABLE I.—(contd.)

1951 (contd.)			1952 (contd.)			1952 (contd.)		
Record.	Date.	Ratio.	Record.	Date.	Ratio.	Record.	Date.	Ratio.
<i>October</i>			<i>February (contd.)</i>			<i>May (contd.)</i>		
42V	1/3	4.5	63W	14/16	4.8	67W	29/31	4.4
38G	1/2	5.0	106K	15/17	5.1	66X	29/31	5.6
57W	11/13	4.5	62W	16/18	4.7	35T	31/1	5.0
16J	13/15	4.5	182R	17	4.5			
58W	15/17	5.0	32T	26/27	5.0	<i>June</i>		
102K	19/21	4.8				18J	31/2	4.2
178R	21	4.2	<i>March</i>			48V	9/12	5.1
43V	29/30	4.3	161C	29/1	5.0	185R	15	4.8
39G	29/30	4.2	181B	5/6	5.3	19J	19/20	4.8
28T	29/30	5.2	62X	6/7	6.2	112K	20/22	5.4
			5H	6/8	4.0	164C	21/22	4.7
<i>November</i>			64W	8/10	4.7	68W	21/23	4.9
59W	3/5	4.0	102A	11/12	4.8	67X	21/23	5.7
61X	5	5.0	107K	14/16	5.5	184B	21/22	5.1
159C	18/19	4.9	6H	25/26	4.6	43G	27/28	4.5
60W	22/24	5.3	63X	29/31	5.3	104A	28/29	5.1
41M	22/24	5.7	108K*	29/30	3.3	36T	29/30	4.2
103K	23/25	5.5	43M	30/31	5.4			
178B	24/25	4.9	33T	31/1	7.0	<i>July</i>		
179R	24/25	4.1				49V	7/9	4.5
29T	29/30	5.2	<i>April</i>			68X	10/12	4.8
			109K*	5/6	4.1	69W	10/12	5.4
<i>December</i>			46V	7/9	4.3	45M	15/17	6.0
40G	12/13	4.8	182B	10/11	5.6	113K	19/20	5.3
104K	14/15	4.9	110K	12/14	5.3	165C	19/20	5.3
30T	27/28	6.4	183R	13	4.2	105A	19/20	4.8
179B	28/29	4.6	7H	16/18	4.6	185B	19/20	4.9
180R	30	4.7	65W	17/19	4.9	186R	20	4.2
			64X	17/19	4.9	37T	31/1	4.7
			162C	20/21	4.8			
			34T	30/1	5.3	<i>August</i>		
1952			<i>May</i>			70W	2/3	4.2
<i>January</i>			42G	2	4.8	69X	2/4	6.1
2H	1/3	5.4	47V	5/6	4.3	50V	11/14	5.0
160C	5/6	4.8	17J	8/9	4.7	166C	16/17	4.9
41G	12/13	5.2	183B	8/9	5.9	114K	16/17	5.3
105K	18/20	4.8	65X	9/11	5.2	186B	16/17	5.6
180B	19/21	5.1	163C	10/11	5.1	187R	16/17	4.1
181R	20	4.3	66W	10/11	5.0	21J	21/22	4.8
42M	23/25	5.7	111K	10/11	5.8	70X	21/22	5.2
3H	24/26	5.0	184R	11	5.2	71W	23/25	4.7
61W	25/27	5.4	44M	14/15	5.5	106A	23/24	5.1
31T	28/29	5.3	103A	24/25	5.1	46M	29/31	5.7
<i>February</i>						38T	30/31	5.8
45V	5	4.7						
4H	12/13	4.0						

TABLE I.—(contd.)

1952 (contd.)			1952 (contd.)			1952 (contd.)		
Record.	Date.	Ratio.	Record.	Date.	Ratio.	Record.	Date.	Ratio.
<i>September</i>			<i>October (contd.)</i>			<i>November (contd.)</i>		
51V	8/10	5.0	188B	12/13	5.0	74X	9/11	6.0
71X	11/13	5.5	189R	12	4.5	169C	21/23	4.9
72W	11/13	5.2	52V	14/15	4.6	189B	23	4.8
115K	13/14	6.1	108A	14/15	5.0	190R	23	4.1
187B	13/14	4.8	40T	15/16	6.1	109A	29/30	5.0
22J	13/15	4.6	116K	18/19	5.6			
188R	13/14	4.7	73X	18/19	5.8			
167C	21/22	5.2	168C	19/21	5.6	<i>December</i>		
107A	27/28	5.5	47M	22/23	5.8	118K	13/15	5.0
72X	28/30	5.2				54V	16/18	4.4
			<i>November</i>			75X	18/19	5.1
<i>October</i>			41T	31/1	5.3	170C	19/20	5.1
39T	1/2	5.2	117K	7/9	6.1	191R	21	3.4
73W	4/6	5.2	53V	9/11	4.6	76W	23/26	4.9

EXPLANATION OF PLATES I TO VI.

Monthly charts of the Recorder tows taken between January, 1950, and December, 1953. The position and extent of each record is shown by a line against which is placed its serial number and route letter. The date, or dates, on which each tow was made can be found by reference to Table I (p. 3-6). The half arrow-head at one end of the line indicates the direction of the tow, and those parts of a record taken between sunset and sunrise are shown by a thicker line than those taken during the day-time.

Here and there, when more than one record was taken over the same route in a month, it has been necessary to displace a record on the chart ; then, arrows at each end of the line indicate its correct position.

Certain records, on which the plankton has not been fully analysed, are not illustrated ; they are shown merely by their serial numbers thus—+ 84K.

PLATE I.

Plankton Recorder lines, January to June, 1950

PLATE II.

Plankton Recorder lines, July to December, 1950

PLATE III.

Plankton Recorder lines, January to June, 1951

PLATE IV.

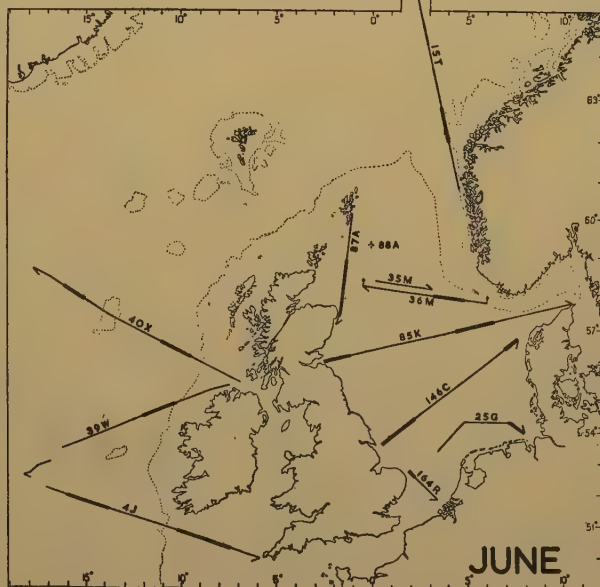
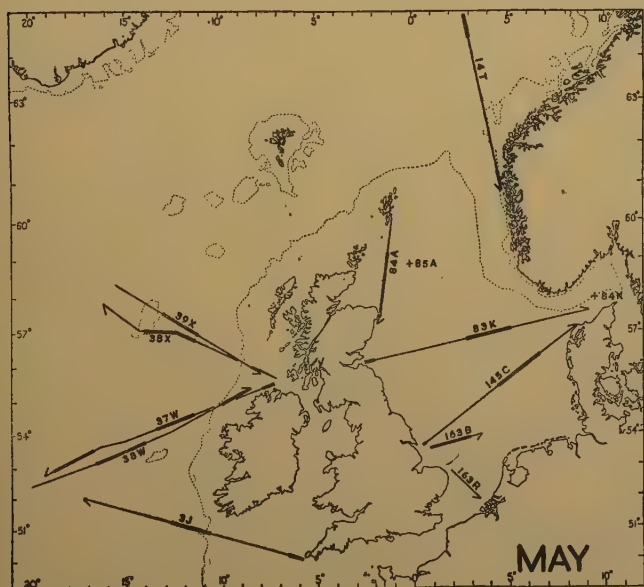
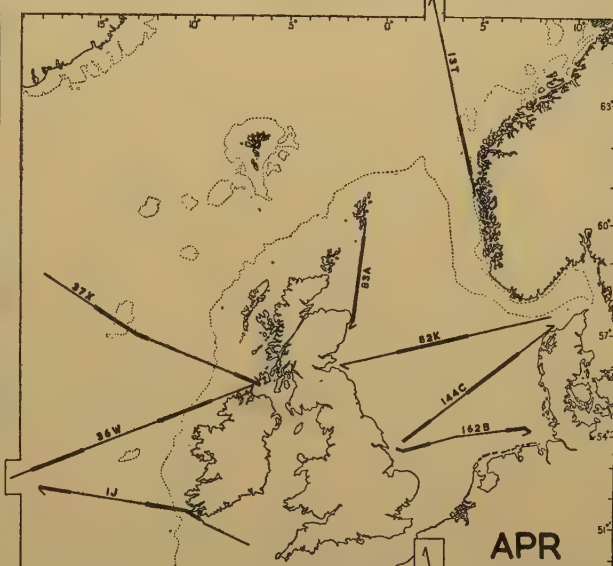
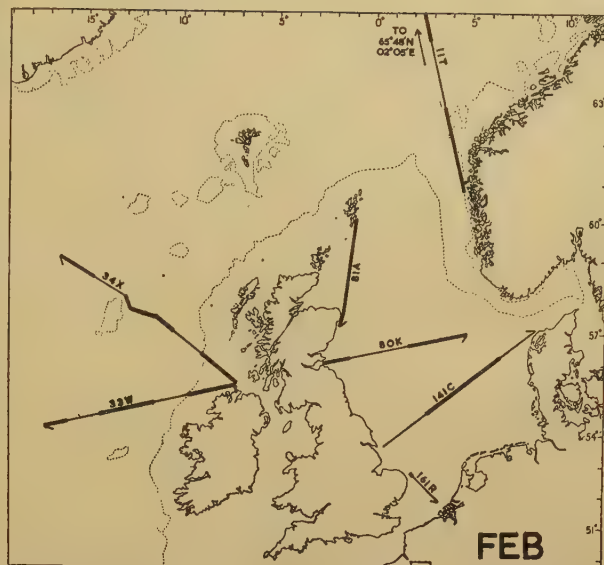
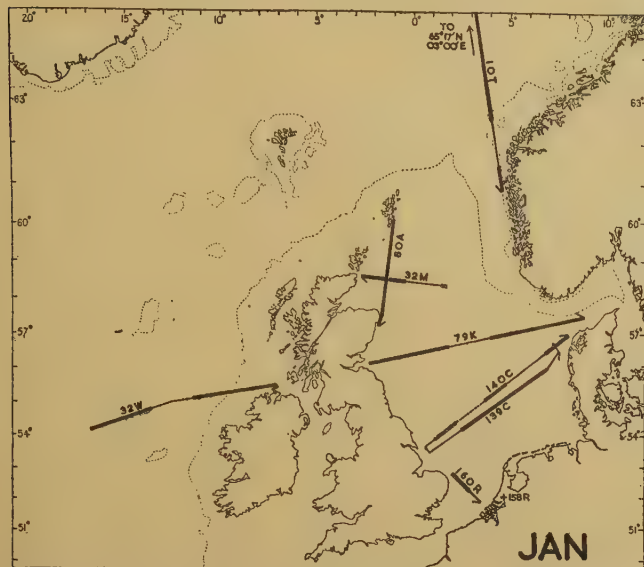
Plankton Recorder lines, July to December, 1951

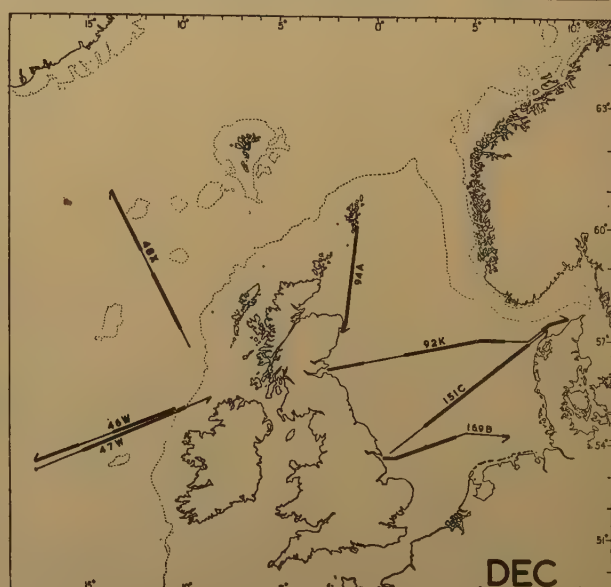
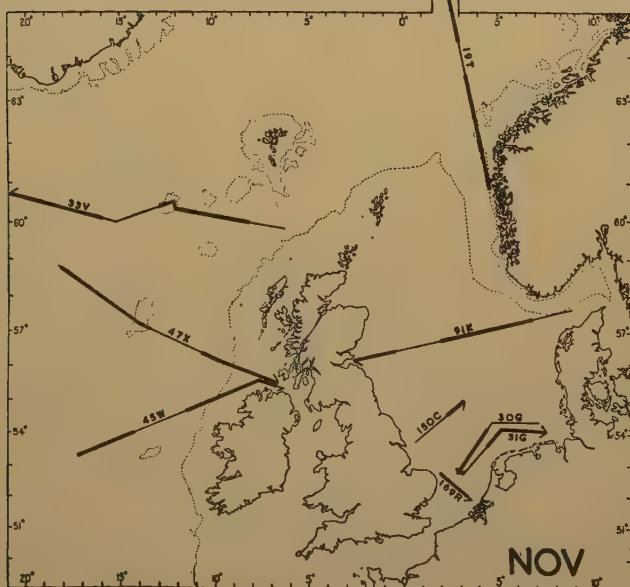
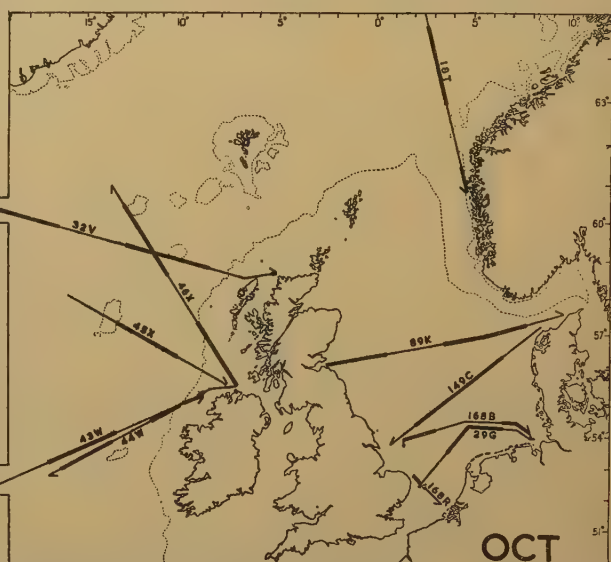
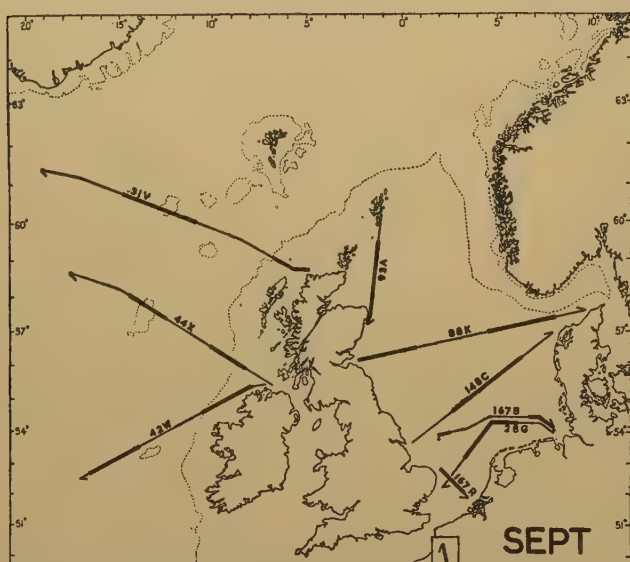
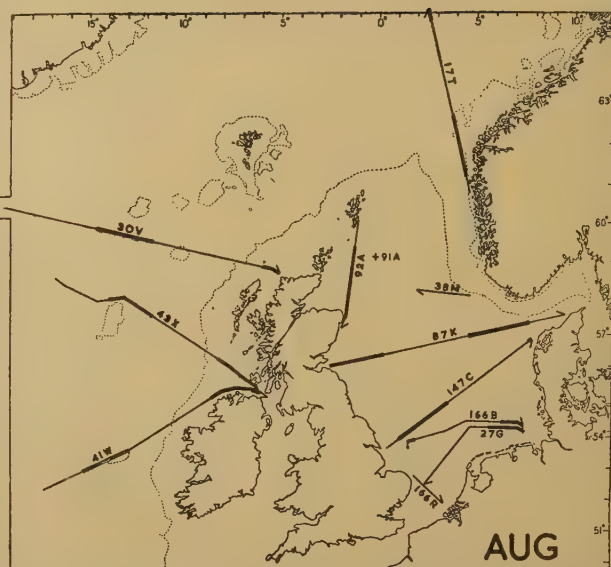
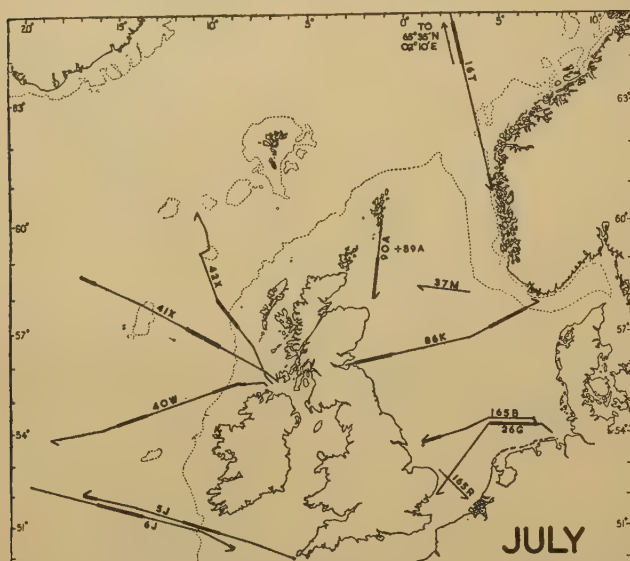
PLATE V.

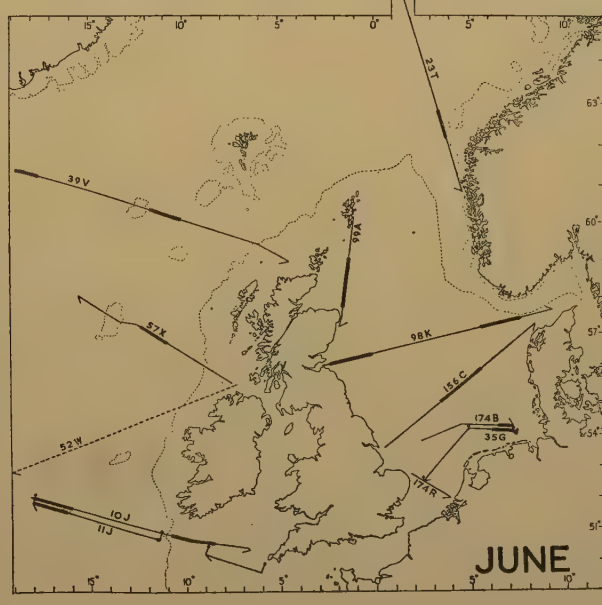
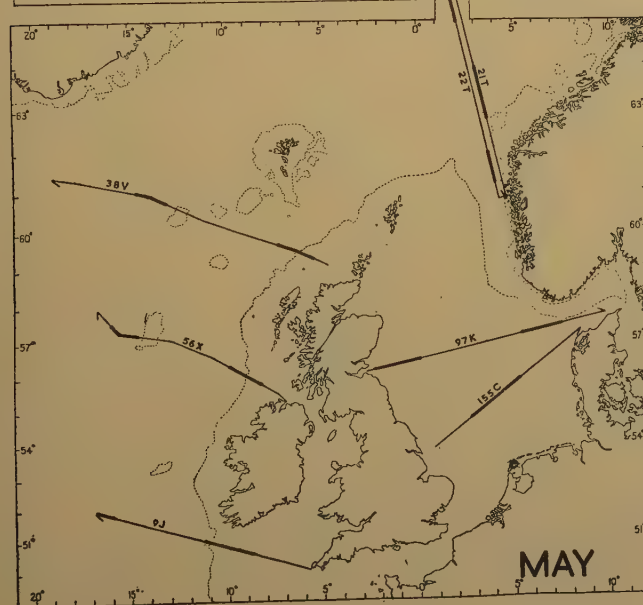
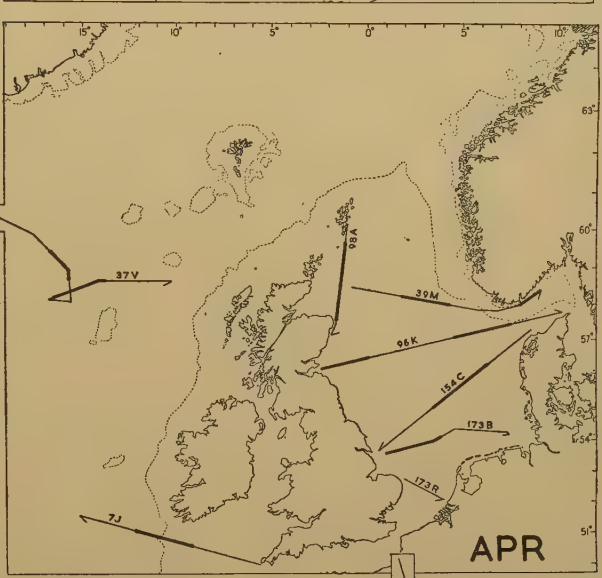
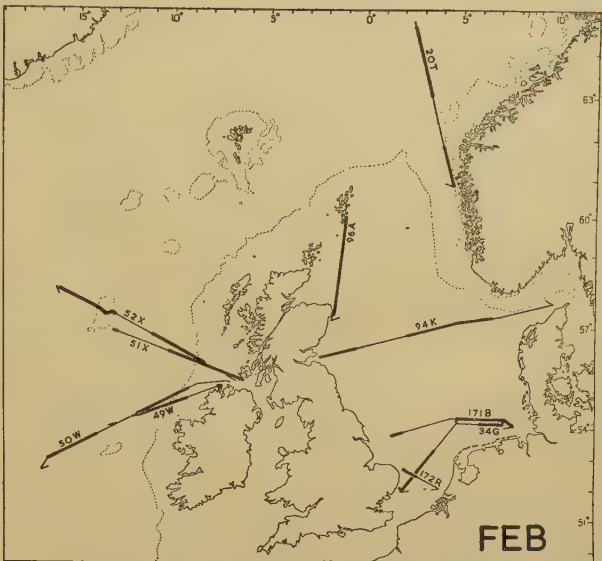
Plankton Recorder lines, January to June, 1952

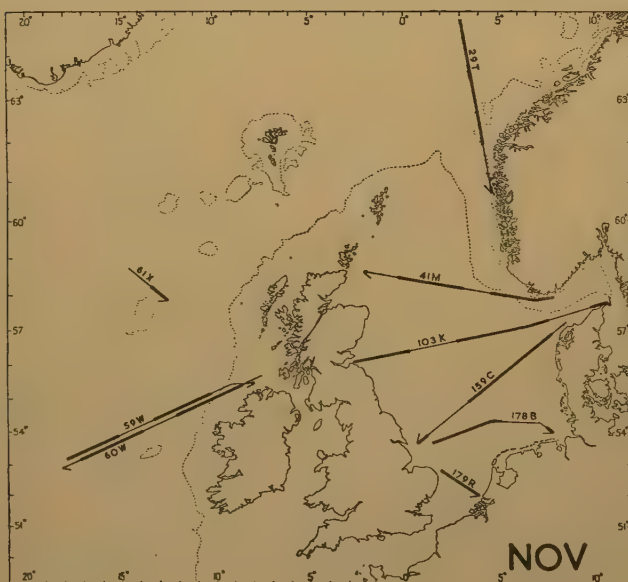
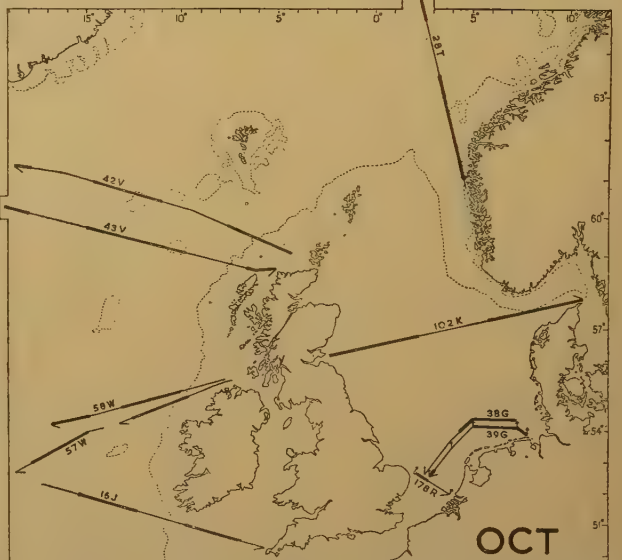
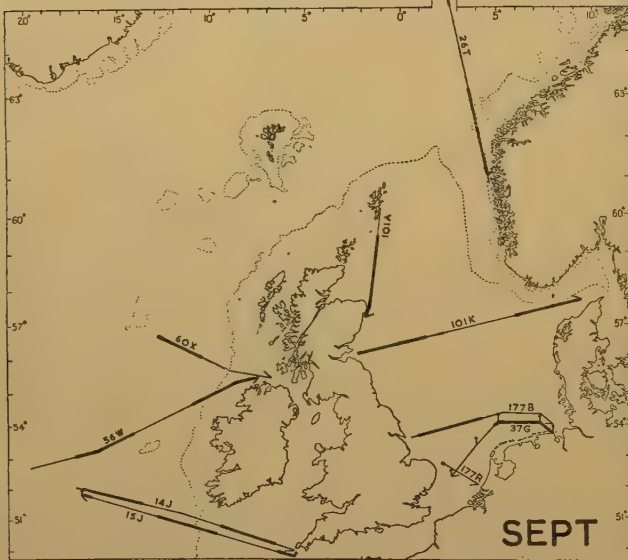
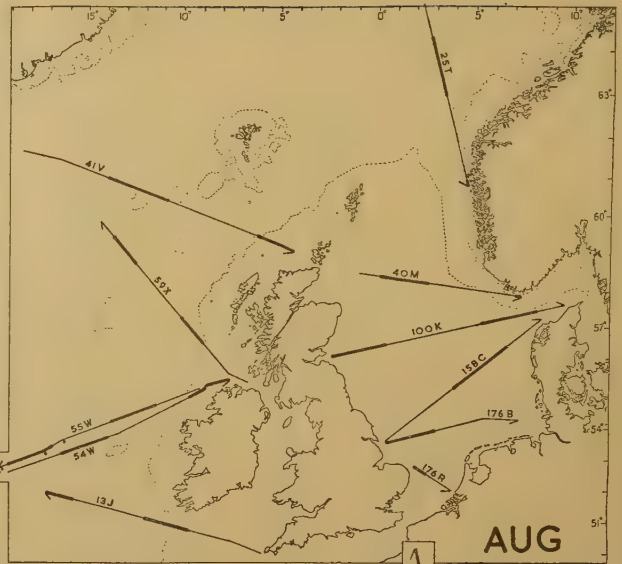
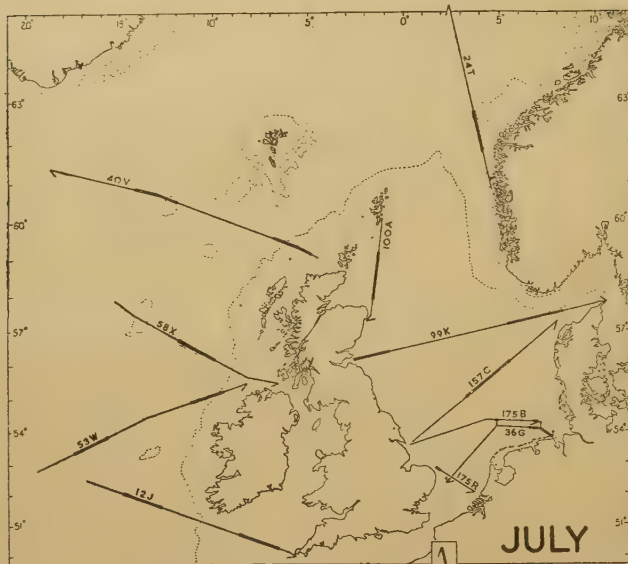
PLATE VI.

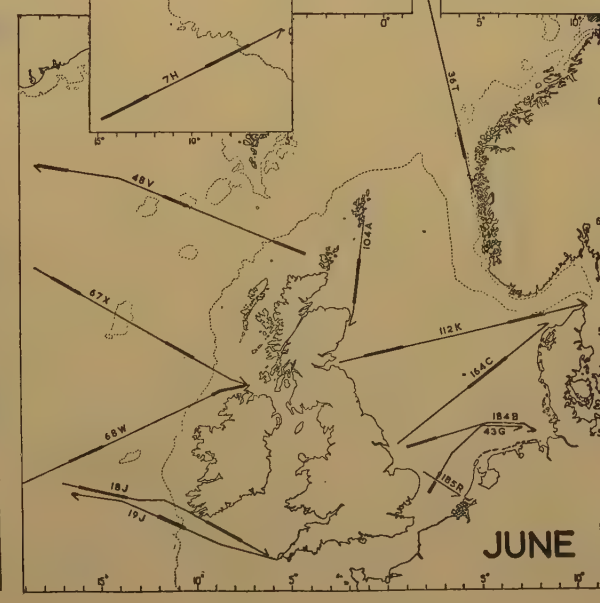
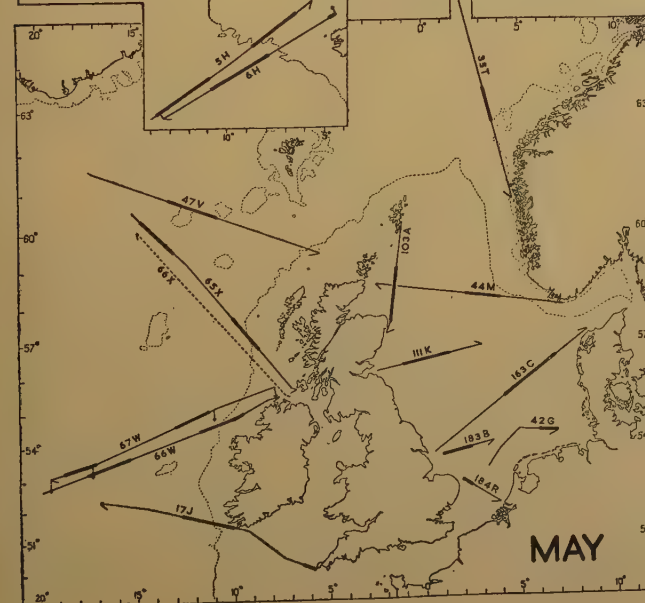
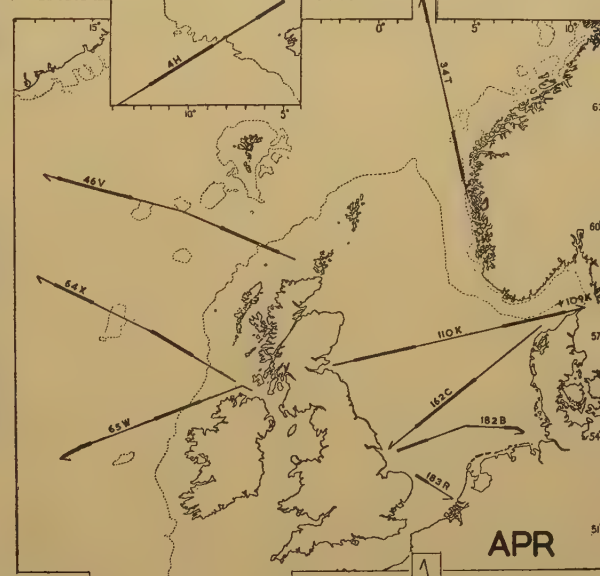
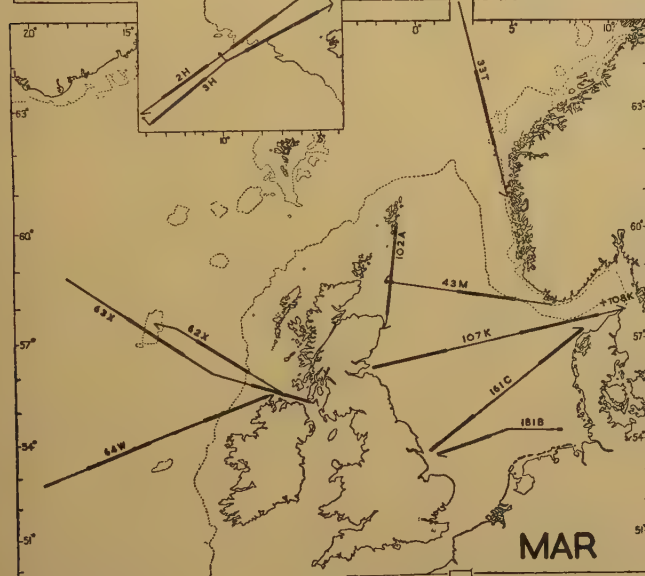
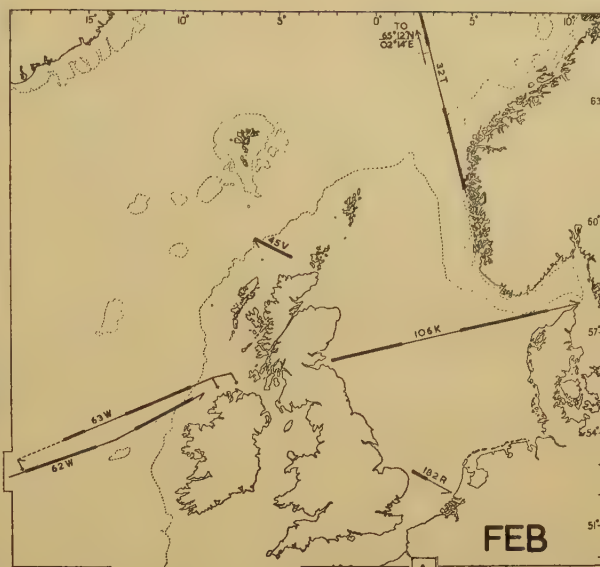
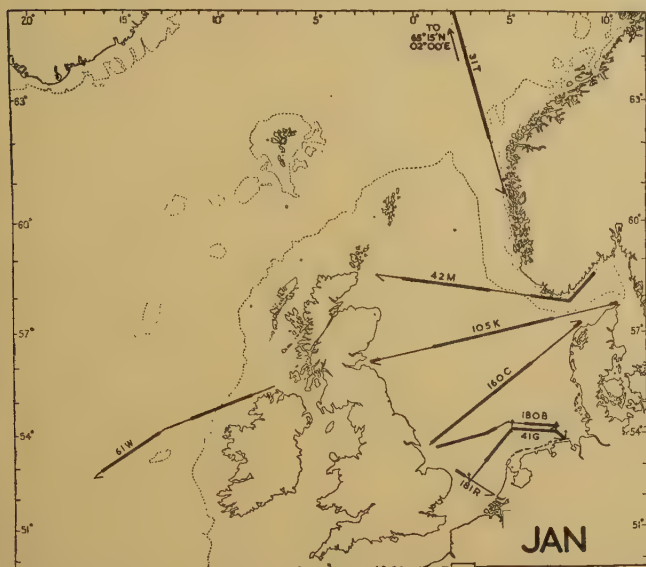
Plankton Recorder lines, July to December, 1952

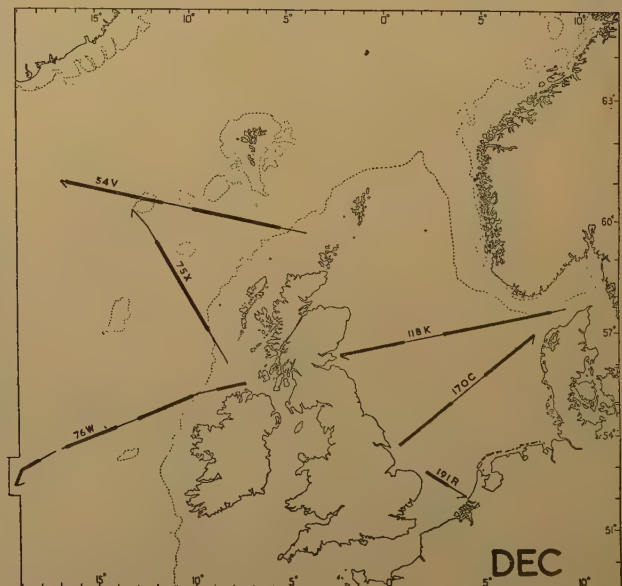
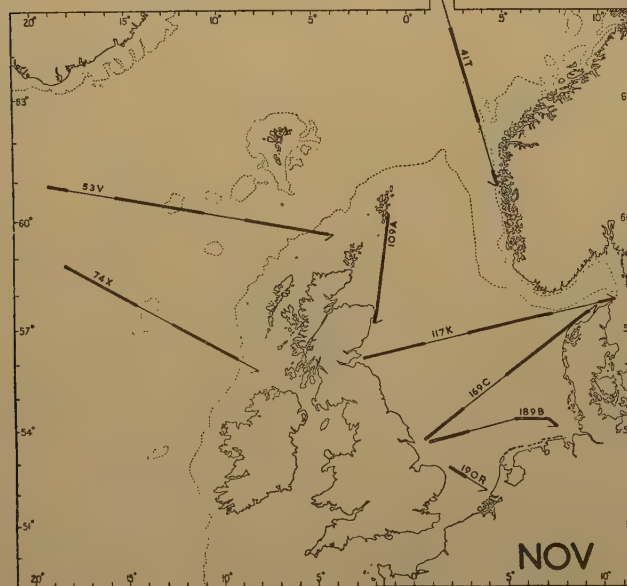
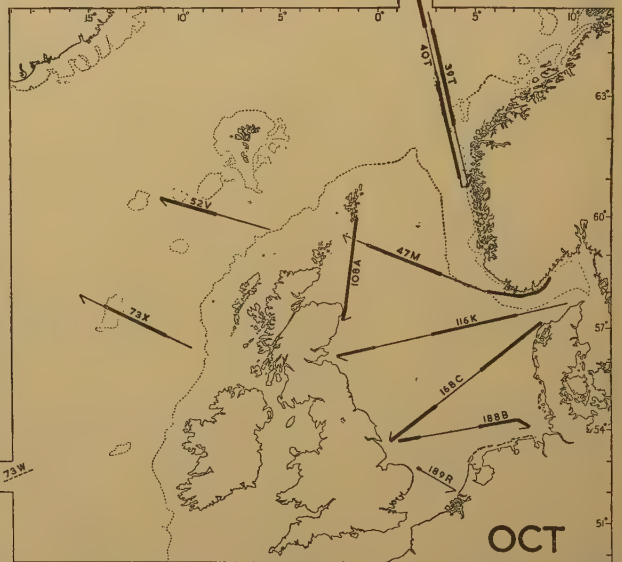
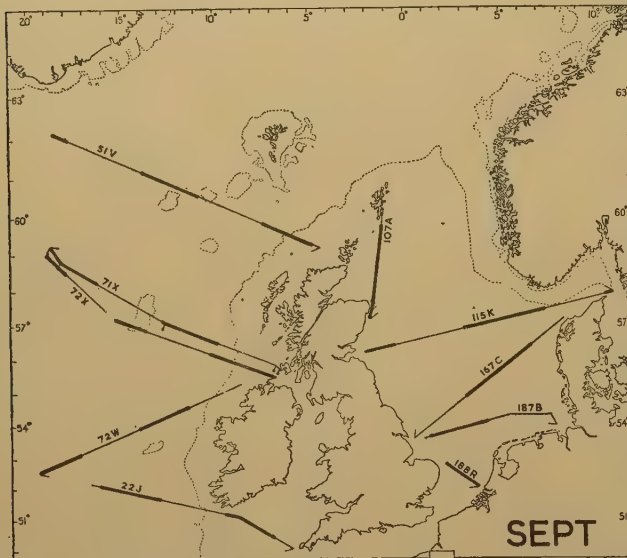
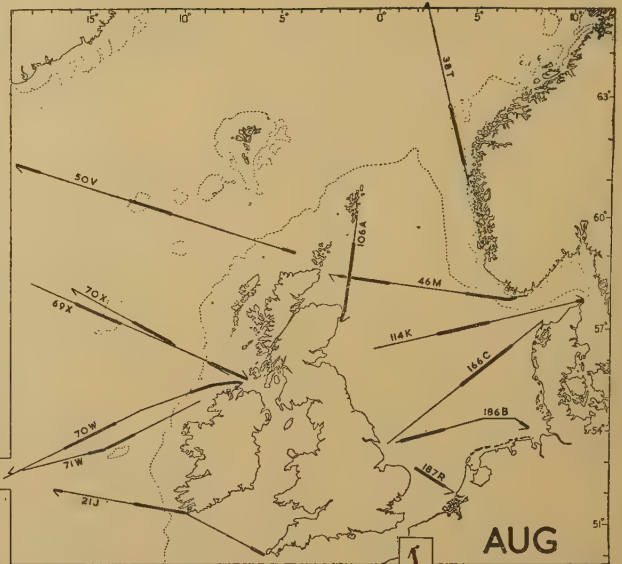
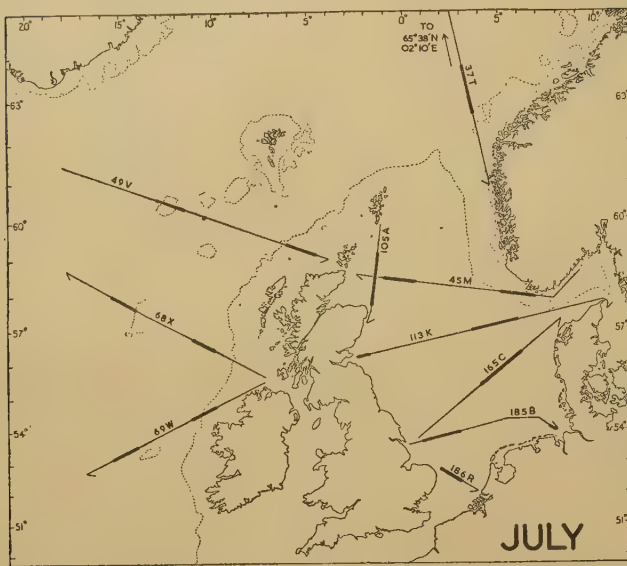












THE HARDY PLANKTON INDICATOR
AND SAMPLER:
A DESCRIPTION OF THE VARIOUS
MODELS IN USE

BY

R. S. GLOVER, B.Sc.

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INTRODUCTION.

SOME thirty years ago Professor A. C. Hardy designed the horizontal sampler which he called the Plankton Indicator. His object was to enlist the assistance of commercial herring drifters to determine whether the quantity and quality of the plankton could be related to the number of herrings to be found in the immediate vicinity. The essential requirement was that the device should be “ . . . simple, strong, easily handled and rapid in use.”

Hardy’s preliminary experiments in 1922 and 1923 (Hardy, 1926) were most encouraging, and when the opportunity occurred he instigated a large-scale survey from the University College, Hull. The Standard Indicator, a modified form of the original pattern, was used for this work which covered the Scottish, Northumbrian and East-Anglian fisheries from 1930 to 1933 (Hardy, Henderson, Lucas and Fraser, 1936). He introduced a further modification in 1934 for studying phytoplankton in relation to the herring (*loc. cit.*). After the recent war yet a further modification was employed when Hardy’s work on the herring and its animate

environment was continued, first from Hull and later from the Edinburgh laboratory of the Scottish Marine Biological Association. The standard Indicator has been used during herring investigations off the Icelandic coast by Fridriksson (1944) and by Einarsson (1951). Gardiner (1933) used it in a study of the vertical distribution of *Calanus finmarchicus* in the North Sea, and as a plankton survey instrument it was used by Gibbons and Fraser (1937) in the northern North Sea, and by Williamson (1952) in the Irish Sea. Erdmann (1937) designed an instrument similar to Hardy's, but with the addition of a closing device and adjustable diving planes which permitted its use at deep, intermediate and shallow depths. Other patterns of the Indicator may have been used elsewhere, and Manteufel (1941) reports that a modified form of Hardy's Plankton Indicator was used in the Barents Sea, but the nature of the modification is not described. To avoid confusion between these instruments it is thought that a brief account of the specifications of the various models will be of value.

In designing the small sampler and introducing recent minor modifications to the small Indicator, the author has received much assistance and advice from his colleagues in the Scottish Marine Biological Association. He is indebted to Dr. Lucas, who in his capacity as Director of Fisheries Research to the Scottish Home Department has permitted the research ships of that department to be used for trials and to take many thousands of plankton samples with the small Indicator. The Scripps Institute of Oceanography generously lent one of their latest type of cable depressor for tests with the small plankton sampler, and much valuable advice resulted from the visit of Mr. K. M. Rae to that laboratory in 1951.

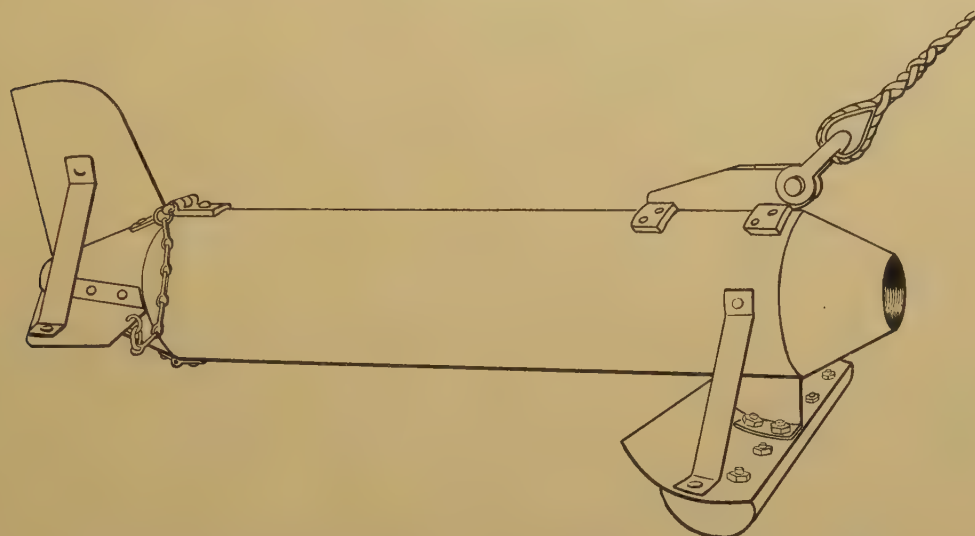
THE VARIOUS MODELS.

The Standard Plankton Indicator.

The prototype Indicator, used in the tests in 1922 and 1923, consisted of a cylindrical tube, the rear of which was hinged to permit the insertion of a disc of bolting silk of 60 meshes to the inch. This instrument, which was nearly 4 ft. long and was carried down in the water by means of a weight attached to the towing line, is described fully by Hardy (1926). Earlier tubular metal plankton samplers, using a weighted line and collecting the plankton on a flat disc of silk, were the Planktonröhre described by Apstein (1906), who mentions an even earlier instrument used by Steenstrup in 1899, and the plankton collector "Etmophor" of Zacharias (1907).

Hardy found that his prototype, which was towed on 60 fathoms of line with a weight of 20 lb., did not reach a sufficient depth to sample the plankton in the region of the herring nets. In 1930, for the extensive survey which was carried out with his colleagues from 1930 to 1933, he designed a smaller instrument (Hardy, 1936). This, the standard plankton Indicator, introduced an important addition to the prototype. Like a paravane, it was fitted with a system of diving-

planes at the front end, and stabilizing planes and a rudder at the rear end (Text-fig. 1). This at once gave the instrument two new advantages; it made it dive and tow with stability several fathoms below the surface, and it removed all towing wires and obstructions from *in front* of the sampling aperture. The standard Indicator dives to a depth of 4 to 5 fathoms when towed on some 20 fathoms of log-line behind a commercial drifter at the normal "full" speed of about 8 knots. The disc, bearing the catch of plankton, is removed from the machine, after a tow of one mile, by swinging open the hinged rear-end of the barrel. Each sample may then be inspected by a fisherman, using a lens-holder, or it may be returned



TEXT-FIG. 1.—The standard plankton Indicator (fig. 4, Hardy, 1936).

to the laboratory for detailed analysis. Hardy used a disc rather than a conical net so that the instrument could be used to give a rapid indication of the plankton at a glance; it was for this reason that he called his instrument an "Indicator."

The Small Plankton Indicator.

For the investigation into the relationship between phytoplankton and herrings during the East Anglian Fishery, Hardy designed a miniature Indicator for towing whilst the nets were being shot. This miniature Indicator was suspended over the port quarter on 6 fathoms of line whilst the vessel was steaming at 2 knots as the drift nets were shot over the starboard side. It was only 13 in. in length and used a disc with a diameter of 1 in. which was held in place by a screw-in cap at the rear end; for full details, see Henderson, Lucas and Fraser (1936, pp. 281 to 284 and fig. 1). Besides the horizontal diving-planes there were sloping side planes at a marked dihedral angle to give improved stability, and a lead weight under the nose to increase the diving effect.

It was from this model that the small plankton Indicator was developed when, after the recent war, preparations were made to continue the earlier work of Hardy and his colleagues on the ecological relations between herring and plankton. This work was started in 1947, and, in co-operation with the Scottish Home Department, has developed into an extensive ecological survey of the herrings off the north-east coast of Scotland. It was essential that the plankton Indicator should be in use every night from a large number of fishing vessels. During the earlier work with the standard Indicator it had been found that fishermen preferred to shoot and haul the instruments by hand—an arduous task—rather than with a small hand winch which was provided. In order to reduce the labour by fishermen who voluntarily assist in the work the small Indicator was designed.

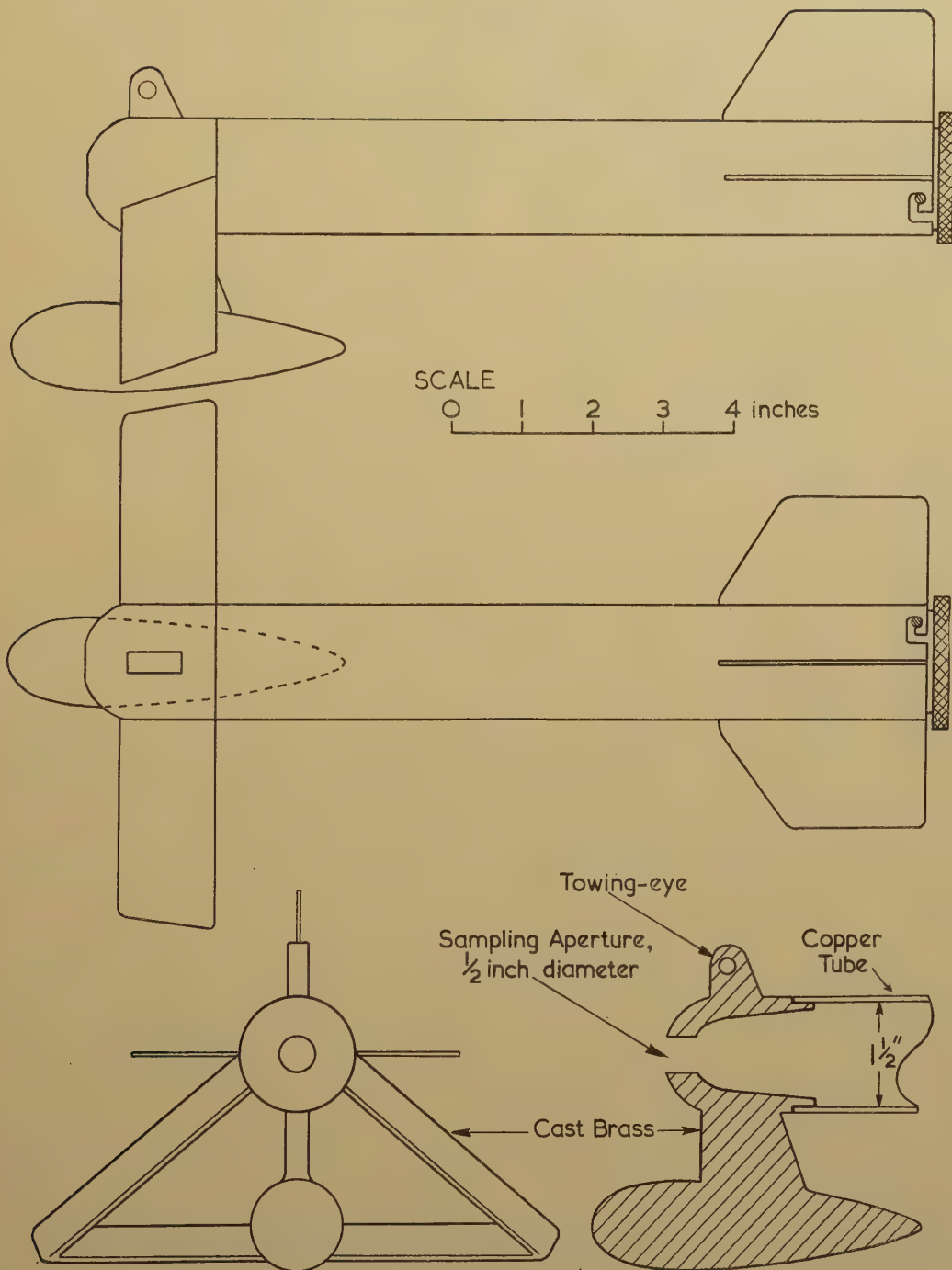
This instrument is essentially like the miniature Indicator but has larger opening, barrel diameter and disc to take zooplankton as well as phytoplankton. Table I provides a comparison between the present machine and the standard Indicator.

TABLE I.—*Specifications of the Standard Indicator and the Small Indicator.*

	Overall length.	Weight.	Diameter of—		Length of towing line.	Depth of tow.
			Sampling aperture.	Collecting disc.		
Standard Indicator .	22 in.	12 lb.	1½ in.	3 in.	about 20 fathoms	8–10 metres
Small Indicator .	12 in.	3 lb.	½ in.	1¼ in.	15 fathoms	7–8 metres

The small Indicator which has been used during the last six years off the Scottish north-east coast is, except for modifications to be described, shown in Text-fig. 2. The nosepiece, towing eye and diving weight are of brass, cast in one piece, with brackets for the attachment of galvanized iron diving-planes. These diving-planes, consisting of a horizontal plane and two sloping side struts, are canted at an angle of about 12° from the horizontal, to give the required diving effect. The tail planes and rudder, as well as the diving planes, are constructed of No. 19 gauge galvanized iron.¹ The barrel is a copper tube with an internal diameter of 1½ in. and with walls $\frac{1}{32}$ in. thick; it fits tightly over the nose-casting, to which it is screwed and soldered. These materials are sufficiently robust to withstand normal usage, but are sufficiently flexible to permit manual adjustment of the planes to correct for any mis-alignment which may develop in use. The sample disc is held in position in the Indicator by a bayonet-fitted brass cap, which presses the disc against a coiled phosphor-bronze spring soldered to a stop-ring inside the barrel.

¹ Some of the instruments were fitted with diving planes, rudder and tail planes of No. 19 gauge copper, but this was found to be too flexible to stand up to the rough usage which Indicators inevitably suffer.



TEXT-FIG. 2.—Side, plan and front views of the small Indicator with a longitudinal section of the front end.

The collecting disc used during the past six years, and still in use, consists of a piece of 60-mesh silk secured to a brass ring by a cellulose-acetate adhesive.¹ The brass ring fits freely in the barrel, being $1\frac{7}{16}$ in. external diameter, with a square cross-section of $\frac{3}{32}$ in.; it leaves a sampling area of $1\frac{1}{4}$ in. diameter (Text-fig. 3). An alternative type of disc has sometimes been used in both the standard and small Indicators; this consists of a brass ring with a spring clip of the type used for the net in the small sampler (Text-fig. 5a). With this ring a piece of silk can rapidly be attached or removed at sea, making it unnecessary to prepare a large supply of discs before a survey.

During the present study of the Scottish herring fisheries the small Indicator is towed on a 15-fathom line, composed of $7\frac{1}{2}$ fathoms of thin wire cable attached to the Indicator, joined to $7\frac{1}{2}$ fathoms of hemp fishing line which is used to facilitate hauling.² At speeds of the order of 7 to 9 knots the Indicator tows steadily with the junction between the wire and hemp just below the surface. The work of hauling the machines would be much easier if hemp line could be used without any wire. It was found, however, that the drag resulting from the hemp line, nearly $\frac{1}{4}$ in. in diameter, caused the machine to swim too near the surface and with a considerable loss of stability.

Repeated tests with Kelvin sounding tubes gave very constant readings which were less than the normal usage of the Kelvin scale, but which were interpreted as being between $3\frac{1}{2}$ and 4 fathoms. Allowing for the unconventional use of Kelvin tubes, it may be said that, at the speeds used in these tests, 7 to 10 knots, and using a 15-fathom towing line, the small Indicator samples at a depth of 7 to 8 metres. The Indicators usually swim steadily at this depth; any instability is immediately noticed, for the Indicator leaps to the surface, yawing from quarter to quarter. This characteristic is a useful one, in that it is easy for fishermen to detect and, by adjustment of the planes, to eliminate the only kind of failure which is known.

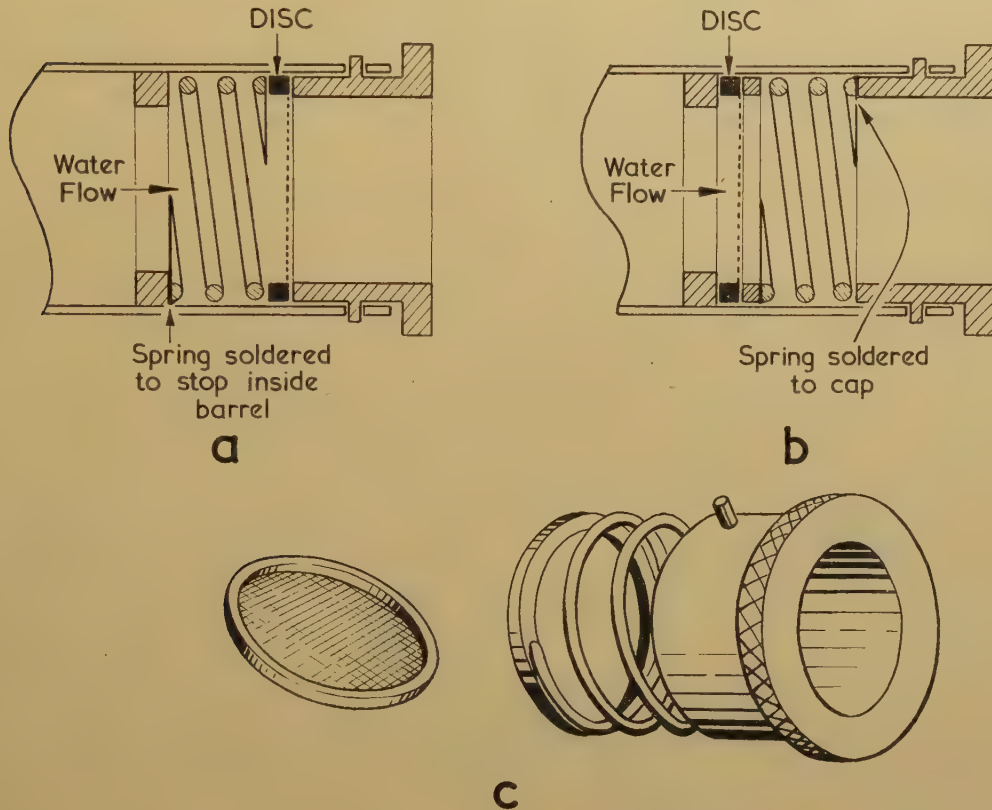
The latest type of small Indicator, which is illustrated in Text-fig. 2, incorporates two modifications of the instrument described above. These modifications apply to—

(a) *The nose-cap*.—The diving-planes are now cast of brass as part of the nose-cap. This modification has been introduced with the object of producing strong diving-planes which are absolutely symmetrical and identical on different machines: objectives which were not so easily achieved when galvanized iron planes were cut and fitted by hand. The brass planes, being over twice as thick as the galvanized iron, increase the drag due to frontal resistance; to compensate for this and to add greater stability, the angle of attack of the diving planes has been increased to 18° .

¹ Celluloid cuttings are dissolved, or the commercial product "Durofix" is diluted, in amyl acetate to make a free-running solution; the brass rings are dipped in this and laid on pieces of silk, the edges of which are later trimmed. This method is satisfactory except when discs are stored for over a year or in damp conditions, which cause some detachment of the silk from the brass ring.

² The wire is $\frac{1}{8}$ in. diameter galvanized plough-steel of 7/14 construction, and with a nominal breaking-strain of half a ton. The fishing line is barked hemp, weighing 4 lb per 60 fathoms.

(b) *The tail-cap.*—In the model described above there must always have been minor leaks of water between the edge of the disc and the sides of the barrel (Text-fig. 3*a*). If such leaks were constant and small they could probably be ignored, but it was noticed that after prolonged use the barrel sometimes became “swollen” in the region of the bayonet slots. Further, without care in machining the cap to fit each barrel with exactly the same degree of freedom, there was a risk of variable



TEXT-FIG. 3.—(Above) Longitudinal sections of the rear-end of the barrel of the two types of small Indicator, showing, *a*, the fitting used during the past six years and *b*, the improved fitting now in use. (Below, *c*) A small Indicator disc and the improved spring cap detached from the barrel.

leaks between the cap and the sides of the barrel. Since the diameter of the copper tubing which is used shows some variation, it was decided to fit the coiled phosphor-bronze spring to the cap, instead of soldering it to the inside of the barrel. Text-fig. 3, *b* and *c*, shows the cap in its new form. A brass disc-ring, without the silk, is soldered to the open end of the spring. The collecting disc, instead of being pushed against an open spring in front, is now pushed from behind by a spring which holds the disc firmly against the stop-ring inside the barrel. In this way

no leaks can occur, except through compression of the spring by the pressure of of water on the disc—an unlikely event at towing speeds below ten knots.

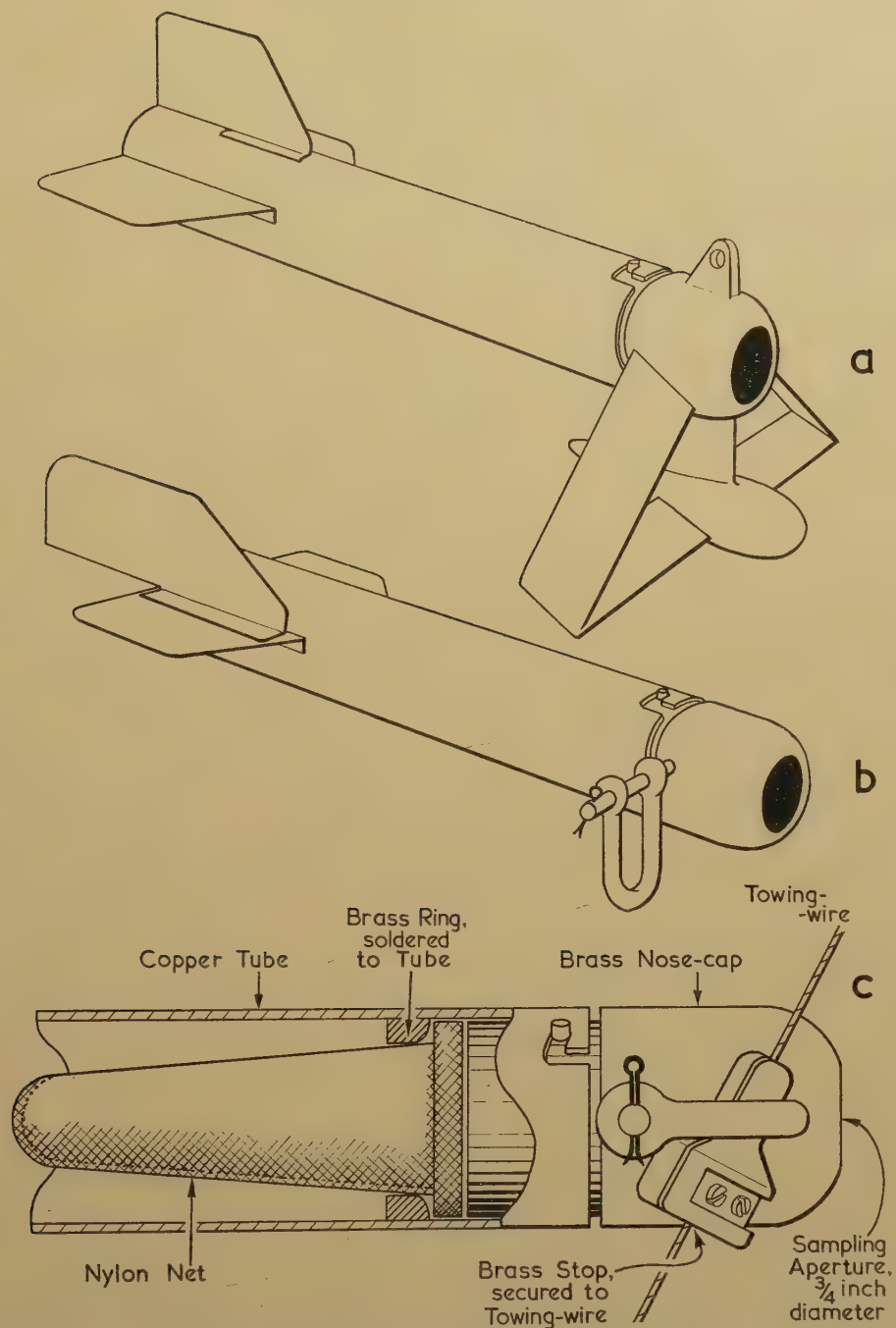
The Small Plankton Sampler.

The Indicator, intended for use in connection with drift-net fisheries, was designed for sampling at about the same depth as the nets which catch the fish. But in a more comprehensive study of herring biology it was realized that information was needed about the plankton at greater depths. A high-speed net which could be used simultaneously at, say, four or five different depths from 10 to 50 metres seemed to be desirable. The silk disc on which the plankton is collected in the Indicators was designed primarily so that fishermen could immediately see the plankton, lying on a flat surface, and could compare it with photographs of "standard" discs. A disc is also convenient for use from fishing vessels in that it is easily handled and stored for return to the laboratory. But when aboard a research vessel with its improved facilities for handling and storing samples, it is probably more satisfactory to catch the plankton in a net with its relatively better filtering qualities and the resultant improved condition of the plankton, and at the same time to collect larger samples than those taken by the Indicator. The small sampler which is illustrated in Text-figs. 4 and 5 has recently been designed and manufactured in the Edinburgh laboratory to fulfil these requirements.

The net itself is held inside a copper tube of the same dimensions as that used in the small Indicator. At the front end of the tube a brass nose-cap fits by means of a bayonet clip. Removal or insertion of the net is achieved by detaching the nose-cap which, in position, holds the net against a ring inside the copper tube.

The nose-cap is made in two forms, with diving planes and a central towing-eye, and without diving planes but with a lateral towing swivel. The first (Text-fig. 4*a*) is used just like the small plankton Indicator for sampling at one depth only. The second (Text-fig. 4*b*) is designed for sampling simultaneously at different depths. In the second type the laterally-placed towing pin is fitted with a shackle which, in operation, rests on a brass stop secured to the wire (Text-fig. 4*c*). Any number of these stops may be fitted at convenient intervals to the wire, which is carried down by a cable depressor. Each net is free to turn in any direction about its own towing-pin and about the stop on the wire. The instruments can be very quickly shackled on, or removed from, the wire as the stops pass over the side of the vessel.

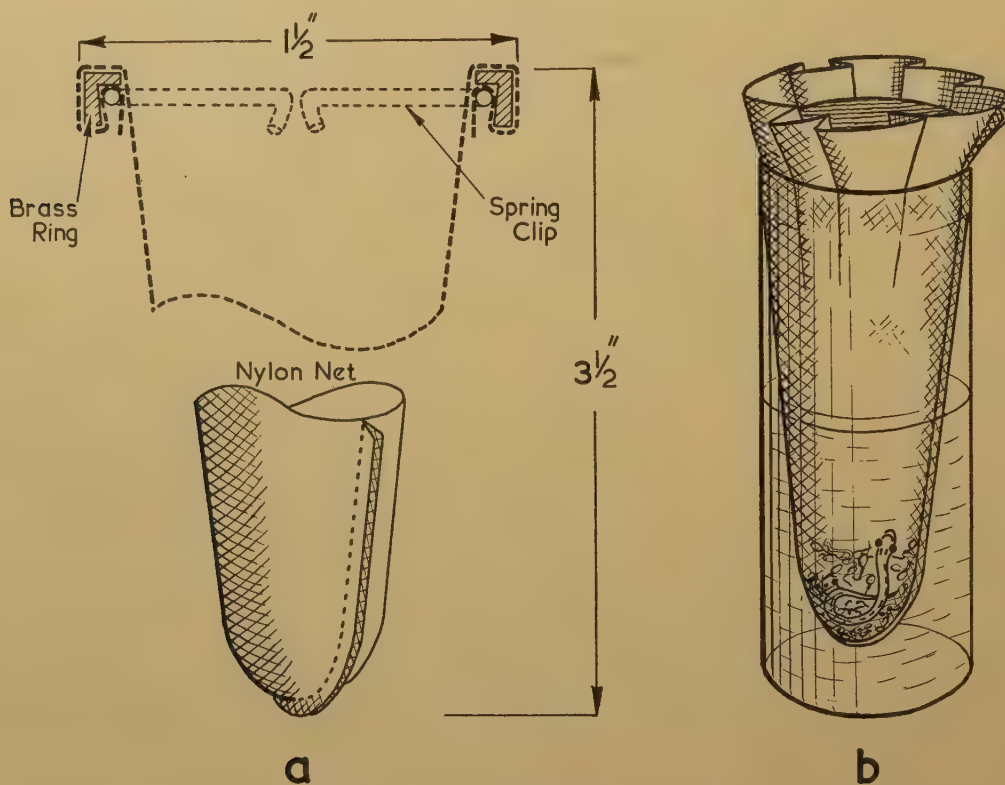
The towing-pin was placed at the side of the barrel in order to leave the sampling aperture free of obstruction by the towing wire or bridles in front of the opening. It was expected that a lateral point of attachment would result in the instrument towing "skew"; for this reason a large rudder was fitted asymmetrically, on the same side as the towing pin. In practice the nets have proved to be extremely stable in the water, and even with the rudder removed there was no visible deviation of the barrel from the true line of towing, although the instrument did appear to "wobble" slightly about the wire.



TEXT-FIG. 4.—The small plankton sampler.

- a.* With diving planes, for use when sampling at one depth.
- b.* Without diving planes, for use when sampling simultaneously from a number of different depths.
- c.* A part-section of the second type, showing the net in position with the instrument resting on the stop fixed to the wire.

The net is made of nylon, with 60 meshes to the inch ; it is $3\frac{1}{2}$ in. long with a diameter at the mouth of $1\frac{1}{4}$ in., and is simply constructed with only a single line of stitching along its length. The free edge is folded over a brass ring of "angle" cross-section, and is held in place by a spring clip (Text-fig. 5a). When the machines are hauled in, the nylon net is removed from the ring and is stored in a small specimen tube as shown in Text-fig. 5b. If the nets are towed for a considerable distance, say 3 miles, the absence of a closing device is not serious as the hauling-up time is relatively small.



TEXT-FIG. 5.—The small plankton sampler.

- a.* A part-section showing the method of attaching the nylon net to the brass ring.
b. Showing the net after use, detached from the ring and stored in a specimen-tube for transport to the laboratory.

Being small, the nets allow efficient depth-keeping qualities with a light wire. So far they have been towed at 7 to 9 knots, with a galvanised wire of $\frac{1}{2}$ in. circumference and a depressor of the type described by Reed and Stewart (1949). With 37 fathoms of wire in the water, and with four small samplers at 10-fathom intervals, a cast-brass depressor, weighing 42 lb., reached a depth of 20 fathoms at a speed of 7 knots.

SOME CHARACTERISTICS OF THE INSTRUMENTS.

The standard Indicator discs used in the pre-war surveys were wrapped in calico and stored in formalin for transport to the laboratory. The small discs which are currently in use are placed in a paper envelope of the type used by philatelists. The discs in their envelopes are then kept in a jar or tin over a pad of cotton-waste soaked in formaldehyde. Discs have been satisfactorily preserved in this manner for over a month before analysis.

In the current survey of Scottish herring fisheries analysis is performed with the plankton lying *in situ* on the silk. After analysis, the silk, with its plankton, is detached from the brass ring and stored in a specimen tube in 4% neutral formaldehyde; the brass ring is then available for use with a fresh disc of silk. Storage of the small sampler net in a specimen tube allows the net with the retained plankton to be left undisturbed until the samples are returned to the laboratory. The net can then be everted and the plankton removed without the loss which frequently occurs on the sides of larger plankton nets which must be washed down at sea. After removal of the plankton, the nylon net is ready for use again.

The chief merits of these Indicators and samplers are the ease with which they can be worked at sea without stopping or slowing the towing vessel, the absence of obstruction in front of the opening, the convenience of the collecting discs or nets, and the simplicity and therefore the cheapness of their construction. As many workers have pointed out, sampling at high speed results in a twofold advantage, in that it increases the chances of capturing active animals which might be expected to avoid a slowly moving net, and secondly in that a large number of samples can be taken in the shortest possible time. This last point may be decisive where it is desired to picture the distribution of plankton at frequent intervals of time over a large area of sea.

The price which has been paid for these advantages is the small size of the samples which are usually taken during one to three miles of towing. The standard Indicator as used by Hardy and his colleagues filtered 2 cubic metres of water (Hardy, 1936) and by Williamson (1952), 4 cubic metres. During the present survey of Scottish herring fisheries the small Indicator is towed for approximately $1\frac{1}{2}$ miles and so samples about a third of a cubic metre, and the small sampler in a 3-mile tow filters the plankton in 1.6 cubic metres. It is useful to compare the sampling characteristics of these instruments with those of two other commonly used plankton samplers, the Continuous Plankton Recorder and a conical 1-metre net with a length of, say, 3 metres (Table II).

The small size of the aperture almost certainly excludes many coelenterates and ctenophores and possibly some of the larger planktonic young fish from the small Indicator sample. Barnes (1951), by a statistical treatment of paired hauls, has shown that the coefficient of variation of the small Indicator catches is of the same order as that given by Winsor and Clarke (1940) for pairs of horizontal net hauls of 10 and 15 minutes' duration at 2 knots. Their nets were 12.7 cm. in

TABLE II.—*Relative Sampling Characteristics.*

	Small Indicator.	Small Sampler.	Standard Indicator.	Continuous Plankton Recorder.	Standard one-metre conical net.
Area of sampling aperture	1.27 cm. ²	2.85 cm. ²	11.40 cm. ²	1.61 cm. ²	7854 cm. ²
Area of silk disc or net	7.92 cm. ²	62.05 cm. ²	42.80 cm. ²	51.61 cm. ²	47,124 cm. ²
Ratio : $\frac{\text{Area of aperture}}{\text{Disc or net}}$	$\frac{1}{6.2}$	$\frac{1}{21.8}$	$\frac{1}{3.8}$	$\frac{1}{32.0}$	$\frac{1}{6.0}$
Ratio : $\frac{\text{Area of aperture}}{\text{Effective filtering area}^*}$	$\frac{1}{2.3}$	$\frac{1}{8.1}$	$\frac{1}{1.4}$	$\frac{1}{11.8}$	$\frac{1}{2.2}$

* The holes in the filtering silk occupy about 37% of the total silk area.

diameter at the mouth, and they comment that under the conditions of their investigation these nets were as reliable as nets of 30.5 and 75 cm. in diameter. Except for the loss of larger organisms it is probable that the small sample-size of the small Indicator is not as serious a source of error as it was once feared. Clearly, these machines can be made larger than the models described here; tests will be performed in the near future on a small sampler and on a replica, two or three times as big, in order to estimate variation resulting from small sample size.

Barnes (1951) showed that, taking 75% as a representative coefficient of variation, the confidence limits ($P = 0.05$) for a single count from a single haul with the small Indicator are 33% and 300%. Two tests of nine and six tows with the standard Indicator gave a much lower coefficient of variation, 30%, but this may be related to the disc in this machine, which Barnes suggested is too small in relation to the sampling aperture, whereas the small Indicator disc appeared to be adequate in this respect. He tested this by using a silk net of area equivalent to thirty times the sampling aperture, instead of the normal silk disc; there was no significant increase in the catch of the small Indicator fitted in this way. The proportion of aperture to net of 1:30 which was used in these tests is about the same as that in the Continuous Plankton Recorder which Barnes (1950) also reported to be efficient in a similar test. Read in conjunction with Table II these results suggest that the area of the disc in instruments of this type, using 60-mesh silk, should be at least six times the area of the sampling aperture. The effective filtering area, that is, the summed area of the holes in the silk mesh, is only $1.4 \times$ the sampling aperture in the standard Indicator; this may be insufficient to pass the volume of water presented by the aperture. In the small Indicator the corresponding figure of 2.3 is probably just above the critical value.

At the normal towing speed of 8 knots, and without correcting for the frictional resistance of a grid, it may be said that water passes through the silk at more than $5\frac{1}{2}$ knots in the standard Indicator and at $3\frac{1}{2}$ knots through the small Indicator disc. The small sampler was designed to fall nearer to the characteristics of the Continuous Plankton Recorder in this respect, and it is noticeable that the plankton

is in a quite undamaged condition in the nets of the sampler, whereas it suffers some squashing in the Indicators.

In conclusion it is appropriate to mention that Lohmann, as long ago as 1903, pointed out that no one method of plankton collection is adequate for all types of organism. Ideally, for the largest organisms, huge nets taking large samples were required, for fish eggs and copepods a smaller sample filtered through a finer gauze, whilst for diatoms and protozoa quite small samples would be adequate if they were filtered through the finest possible silk or through filter-paper. Fundamentally, these early *dicta* of Lohmann stand uncontradicted, and it is clear that a single instrument which could simultaneously take all three types of sample would have many applications. The Indicators and samplers described in this paper can conveniently be grouped to construct such a unit. Indeed, Hardy has experimented with the barrel of a miniature phytoplankton Indicator, holding a fine silk disc slung underneath the barrel of a standard Indicator. In the near future a sampler will be constructed carrying three units strapped together, with a common set of diving and tail planes for use at one depth, or with a single towing pivot for use at a number of different depths with a cable depressor. The units comprising this sampler can carry either discs or nets, and will consist of a barrel of the same size as the standard Indicator with coarse silk, one of the same size as the small Indicator with 60-mesh silk, and a miniature phytoplankton barrel with fine silk of, say, 120 meshes to the inch.

SUMMARY.

1. Several slightly different forms of the plankton Indicator have been designed by Professor A. C. Hardy for different purposes. Two of these which are in use are defined :

- i. The standard plankton Indicator, first used in 1930.
- ii. The small plankton Indicator which has been used since 1947, from fishing vessels and research ships during an ecological survey of the herring off the north-east coast of Scotland.

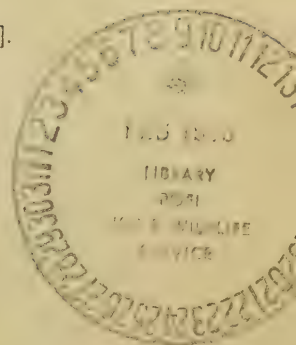
2. A small plankton sampler has been developed from the Indicator design ; it is in two forms, one for use when sampling at one depth, and the other for sampling simultaneously at different depths when several samplers are attached to a single cable towing a depressor.

3. There is a short account of the characteristics of these plankton Indicators and the small plankton sampler.

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CONTINUOUS PLANKTON RECORDS: THE DISTRIBUTION OF LAMELLIBRANCH LARVAE IN THE NORTH SEA, 1950-51

BY

C. B. REES, D.Sc.

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INTRODUCTION.

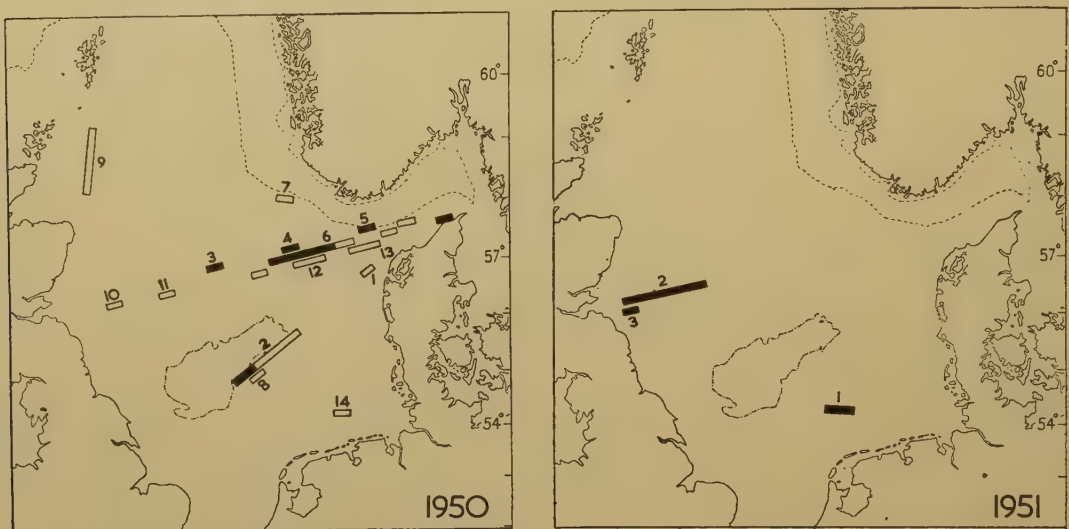
THE distribution of lamellibranch larvae in the North Sea has now been investigated in considerable detail over a period of three years, 1949-51. The distributions found in 1949 have already been presented, although it was fully realized whilst preparing the report that the conditions in that year might have been unusual (Rees, 1951). Many of the identifications of lamellibranch larvae in a previous paper (Rees, 1950) were, however, largely based on the distributions found in 1949 and it was thought that delay in presenting this evidence would be undesirable.

This account of the distributions in 1950 and 1951 is a continuation of the former one and completes the first phase of the investigation. The method of analysis and the derivation of the estimates of numbers have been explained in the first report. From 1952 onwards only major concentrations of larvae will be investigated, a change which will greatly reduce the amount of information acquired. Essentially, only a dozen or so species will be involved in the restricted analysis as against about 50 during 1949-51.

In addition to the Recorder material, the lamellibranch larvae in all Hensen net samples from the North Sea taken in 1950 for the Scottish Home Department, Marine Laboratory, Aberdeen, have been made available to me. It is a pleasure to record my gratitude to the planktologists at Aberdeen for undertaking the tiresome task of extracting the larvae. The contents of these samples will not be fully reported on here but information bearing on specific problems will be used.

DISTRIBUTION OF TOTAL LAMELLIBRANCH LARVAE.

Text-fig. 1 shows, for 1950 and 1951, the distributions of total lamellibranch larvae above the two levels of concentration used in Text-figs. 1 and 2 of the first report (Rees, 1951).

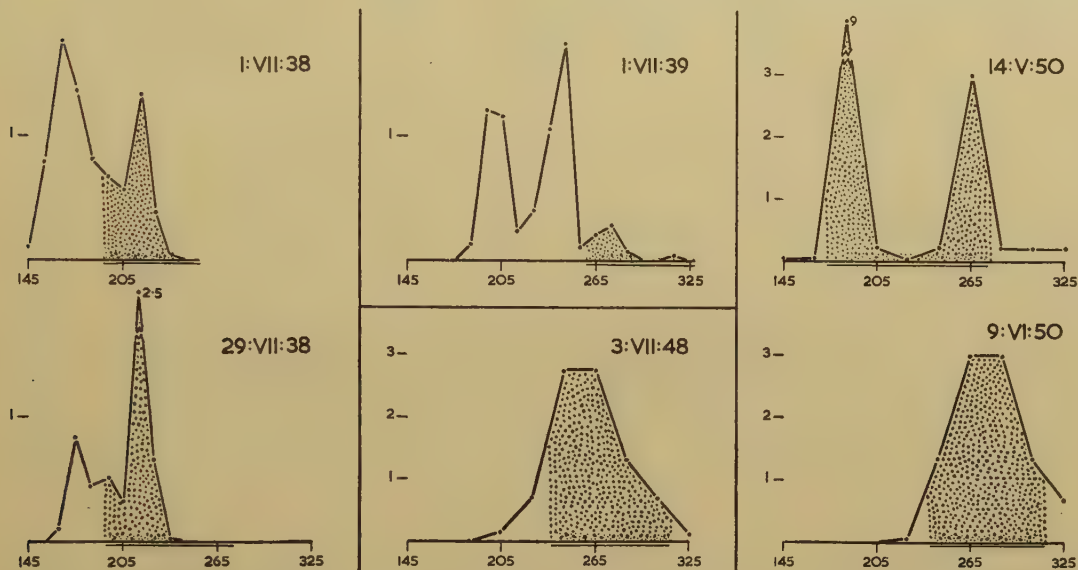


TEXT-FIG. 1.—Charts showing the distribution, in 1950 and 1951, of 10-mile samples with 500–1000 (white rectangles) and more than 1000 (black rectangles) lamellibranch larvae. Patches have been numbered for the purpose of Table III, p. 35.

A patch on the Aberdeen-Lerwick route was found in 1950; such a patch has been found in four years (1938, '39, '47, '50) out of the eight years of Recorder sampling in this area. A concentration off the Forth, with very high numbers of larvae, was found in 1951, and perhaps a minor concentration should be recognized in 1950, comparable with one in 1947. Whilst it can no longer be considered that the patch off the Forth in 1949 was particularly unusual (Rees, 1951, p. 128) it should be noted that the larvae were very much more numerous in 1951 than in 1947 and 1950. We cannot be quite certain about 1949 since the August and September Leith-Skagerrak records were short at the Forth end, but the numbers found on the available samples support the view that the Forth concentration of 1949 was comparable with that of 1951.

A concentration over the Great Fisher Bank was found again in 1950. If we take only the higher level of numbers (over 1000 larvae per sample, equivalent to about 350 per m^3) the years can be classified as (a) Great Fisher Bank patch and no Forth patch recorded: 1938, 1939, 1948, 1950; (b) Forth patch and no Great Fisher Bank patch recorded: 1949 (assumed for Forth patch), 1951; (c) neither patch recorded: 1946, 1947.

It has already been indicated that there is a similarity from year to year in the distributions found within the Great Fisher Bank patch (Rees, 1951, p. 107).

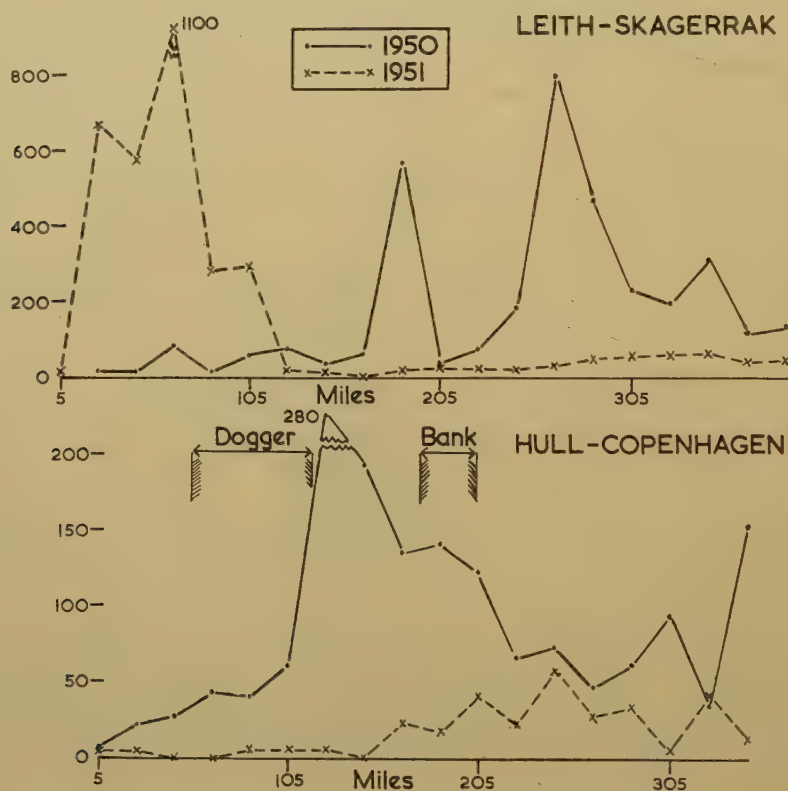


TEXT-FIG. 2.—Graphs giving the number of lamellibranch larvae in each 10-mile sample of a section, 140–330 miles from the Forth, of some of the Leith-Skagerrak records. The vertical scale is in thousands. The parts of the routes sampled between sunset and sunrise are shown by a double base line and the sections of the graphs showing larvae collected at night dotted.¹

The addition of the 1950 results allows more detailed consideration of this point. Text-fig. 2 shows the number of larvae in each 10-mile sample within a section (140–330 miles from the Forth) of each Leith-Skagerrak record that sampled such a concentration. From 1939 onwards there were two positions where peak numbers were found; at a position 190 miles from the Forth and at a position 265 miles away or in one of the two adjacent samples. Two peaks are shown in the 1938 records, one 165–175 miles from the Forth and the other 215 miles away. These two Leith-Skagerrak tows were off the standard route (see Hardy, 1941, plate II)

¹ The distinction between samples taken by night and by day which is made in this and some other text-figures is not considered to be relevant to this report. It is anticipated, however, that this information will be required on a future occasion.

and there is no reason to doubt that the 1938 peaks correspond to the two in 1939 onwards. This occurrence, time after time, of high numbers more or less at the same positions suggests a regular cause. What is particularly noteworthy, apart from the apparent regularity of the pattern, is the sharpness of the peaks. A good illustration is the westerly peak on the record of May 14th, 1950, where the number in one sample exceeded those in the adjoining samples by about 80 and 30 times (Text-fig. 2).



TEXT-FIG. 3.—Graphs giving the average number of lamellibranch larvae per 10-mile sample throughout 1950 and 1951 along the Leith-Skagerrak and Hull-Copenhagen routes. This text-figure corresponds to Text-fig. 3 of Rees (1951).

We shall return to a consideration of this patch later but, meantime, note should be made of the dates. In three years out of four the concentration was found about July 1st. In 1950, however, it was found more than a month earlier, May 14th and June 9th, and it had disappeared from the route by July 7th.

Of the other concentrations in Text-fig. 1, only the patch along the southern edge of the Dogger Bank in 1950 need be mentioned. Attention has been called to a striking consistency in distribution in the recurrence of a narrow patch on the

Leith-Hamburg line in 1938-39 (Rees, 1951, p. 107). The 1950 patch is as near to this earlier one as can be recorded with the routes at present in use.

The average number of larvae per 10-mile sample throughout each of the two years on two Recorder routes is shown in Text-fig. 3. In comparing this with Text-fig. 3 of the first report it should be noted that the vertical scale for the Leith-Skagerrak line has been altered to cope with the much greater numbers obtained in 1950-51. The values for the Hull-Copenhagen route for 1951 are possibly vitiated by the absence of records in September and October; but, if so, it is likely that it is the section between the Dogger Bank and Danish coast which is most affected. Concentrations on the western half of this route have previously been recorded earlier than September.

NOTES ON IDENTIFICATION AND NOMENCLATURE OF LARVAE.

The larvae included in this and the first report were described in an earlier Bulletin (Rees, 1950). Many of these were named specifically, others tentatively, as for example (? *Tellina pygmaea*), and the remainder labelled within a family or superfamily (e.g., Pectinid E). It is now possible to add the descriptions of a few more. The number of illustrations do not really justify the expense of publishing photomicrographs, desirable as this is; instead, line drawings which are tracings of photomicrographs are given. It is also possible to improve and revise some of the labels hitherto adopted. Apart from those items which follow, the same nomenclature has been used in this report as in the earlier descriptive account.

Arcacea.

Glycymeris glycymeris.—A rounder, more symmetrical larva than that described (Rees, 1950) is found occasionally. This is believed to be of the variety *pilosus* (Jeffreys, 1862).

Mytilacea.

MYTILID A.—The widespread distribution of Mytilid A in 1950 and 1951 leaves little doubt that it is the larva of *Modiolus phaseolinus*.

MYTILID F (Text-fig. 4).—The shell is brown and rather convex. The inner edge of the shell is regularly serrated all round except at the hinge and for an arc of about 5° between the dorsal and postero-lateral sides. The fossette for the ligament is deep and central and, in consequence, the intermediate teeth are very small and by no means easy to make out.

MYTILID G (Text-fig. 4).—The concentric lines are fine and close set in shells up to a length of about 320 μ . In larger larvae the outer concentric lines are well-marked and well-separated. A characteristic feature is the presence of irregular external ridges on the shell which disappear in hypochlorite. Several specimens of this species have been found amongst the Aberdeen net samples.

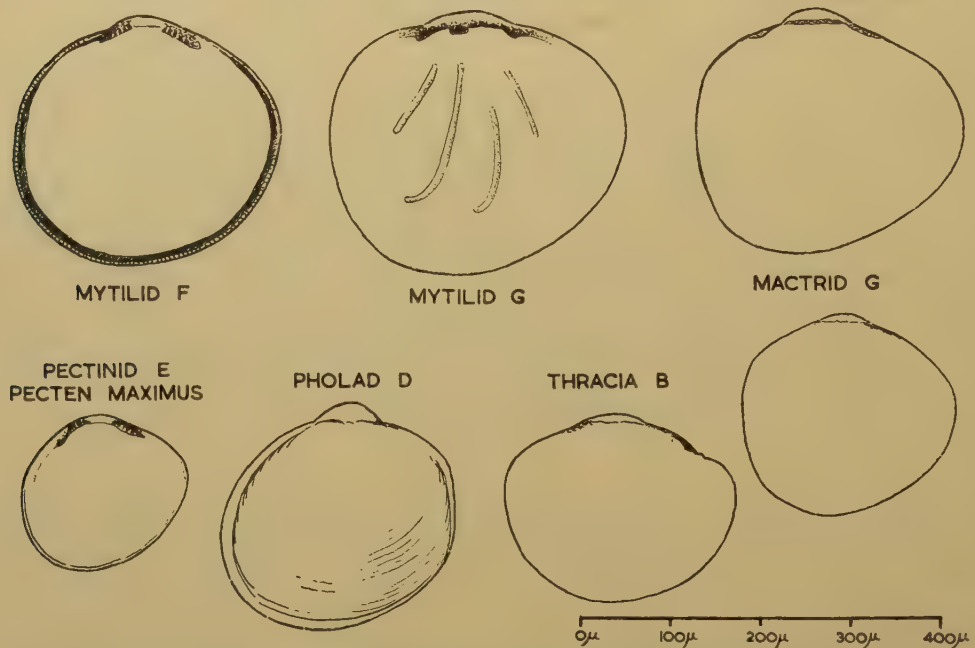
Pectinacea.

PECTINIDS C and E.—It can now be said that Pectinid C is the larva of *Chlamys opercularis* and Pectinid E that of *Pecten maximus*. This has been possible through the kindness of Mr. J.

Mason in supplying plankton samples, young spat stages and information about the spawning of these two species at Port Erin.

It was indicated in the original description that the two specimens shown of Pectinid E might not both be of the same species. It would be best to cancel altogether the smaller of the two photographs; this does not show the backward droop shown by the larger larva and which is distinct even in small larvae (Text-fig. 4).

Paphia.—Quayle (1952) has now published a description of the larva of *Venerupis* (*Paphia*) *pullastra*. This is so like the larva hitherto labelled as (? *Paphia*) that the identification may now be regarded as correct. Whilst the larva which has been described (Rees, 1950) is very like that of *P. pullastra*, it is advisable to await the descriptions of one or two other species of *Paphia* before identity is accepted.



TEXT-FIG. 4.—Tracings of photomicrographs of larvae which are described in the text.

Mactracea.

MACTRIDS A-D.—The identification of several of the Mactrid species were given tentatively only because the numbers of larvae which had been obtained did not agree with the fauna of the Dogger Bank as found by Davis (1923, 1925). A resurvey of the Dogger Bank (Ursin, 1952) has shown a very different fauna from that found by Davis and, in consequence, there is no further cause to regard the original identifications as merely tentative. The following identifications may be regarded as probable: *Mactra corallina*, *Spisula solida*, *Spisula subtruncata*, *Spisula elliptica*.

MACTRID G (Text-fig. 4).—The larva has a Type C hinge which places it akin to *Mactra corallina* but differs from it in shape. Specimens have sometimes been found in the southern North Sea. If these have been transported from the English Channel, they may possibly be of *Mactra glauca*.

Pholadidae.

PHOLAD D = (? *Panomya arctica*) of Rees (1950) (Text-fig. 4).—The larva previously called (? *Panomya arctica*) was placed in the Saxicavacea on the basis of the hinge structure in one valve only. The hinge in a complete specimen shows that it belongs rightly to the Pholadidae and is consequently relabelled Pholad D.

Pandoracea.

THRACIA A.—This is the larva previously designated as (? *Thracia sp.*).

THRACIA B (Text-fig. 4).—An occasional larva has been found which is sufficiently like (? *Thracia sp.*) to be regarded as an allied species. It is characterized by a distinct notch on the dorsal side of the narrow end.

Probable identification to *Thracia* follows from the fact that no other genus of the Pandoracea is represented by two species in the southern North Sea.

DISTRIBUTION OF THE SPECIES.

The approximate quantitative distribution of larvae is shown in Plates VII–X which are directly comparable with Plates VI–VIII of the first report. The distributions of a few of the uncommon species are given only in the notes below. Little will be said about these charts; they are included for record purposes since, with the end of the detailed study of distribution in 1951, it is unlikely that comparable information will again become available through the Recorder Survey. The records taken during 1950–51 are listed by Rae (1953).

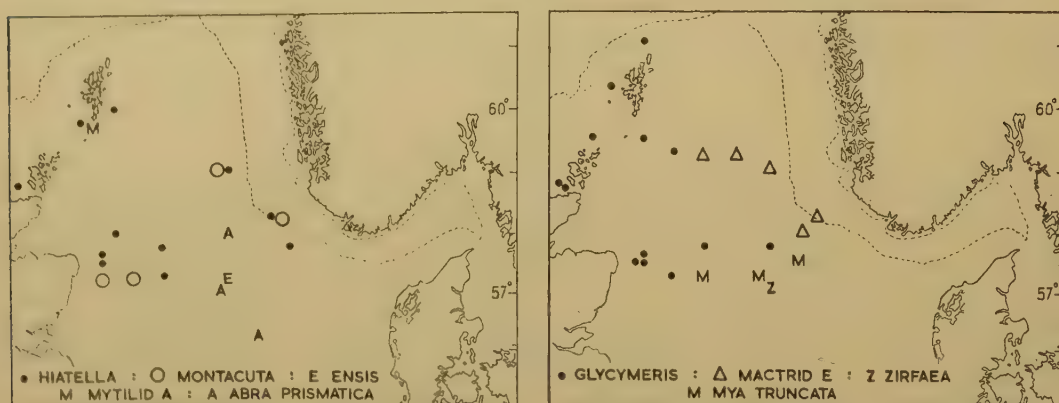
Some information derived from the Aberdeen net sampling is given in Text-fig. 5. The station positions of all samples containing over 50 specimens of various larval forms are shown.¹ *Mytilus edulis* is not included in this text-figure since full information on this species is given later.

Note should be made that the larvae of *Ensis ensis* and *E. siliqua* are here combined under the genus. The distributions of these larvae in 1949 (Rees, 1951) agreed well with the findings of Davis (1923, 1925) and Stephen (1933) that *Ensis ensis* was much more common than *E. siliqua*. However, the estimations for 1950, which was a particularly good year for *Ensis* larvae, give *E. siliqua* as more abundant than *E. ensis*. As will be seen below, some features in the distributions of various larvae early in 1950, particularly of *Mytilus edulis*, suggest a reason for the abundance of *E. siliqua*. On the other hand, it is possible that the material was inaccurately assigned to the two species; it is impossible, unfortunately, to return to the material for revision. In view of the doubt about the accuracy of the estimations, it has been decided to combine the two species and to refer only to the genus.

¹ It should be noted that the numbers of larvae obtained by the Recorder and by vertical net have a different meaning. The number obtained by the Recorder gives the concentration per unit volume of water at 10 m. depth (theoretically 3m³ in a 10-mile sample), whereas the net sample gives the number below a unit area of sea surface (approx. 0.4 m²), both within limits of sampling errors.

Seasonal Occurrence.

Table I gives the seasonal results in the same way as in Table I of the previous report (Rees, 1951, p. 112). For convenience the same order and grouping has been used, but *Mya truncata* has been added to the spring breeders and many species removed, particularly from the list of autumn breeders; the charts (Plates VII-X) contain all the information though in a less convenient form. Interest chiefly centres on species with apparently two breeding seasons in the course of the year. Certainly these species stand out most clearly in groups *d*, *e* and *f* of Table I of the previous report. That this feature is less apparent in the Table here is due on the one hand to the widespread distribution of the species in 1950,



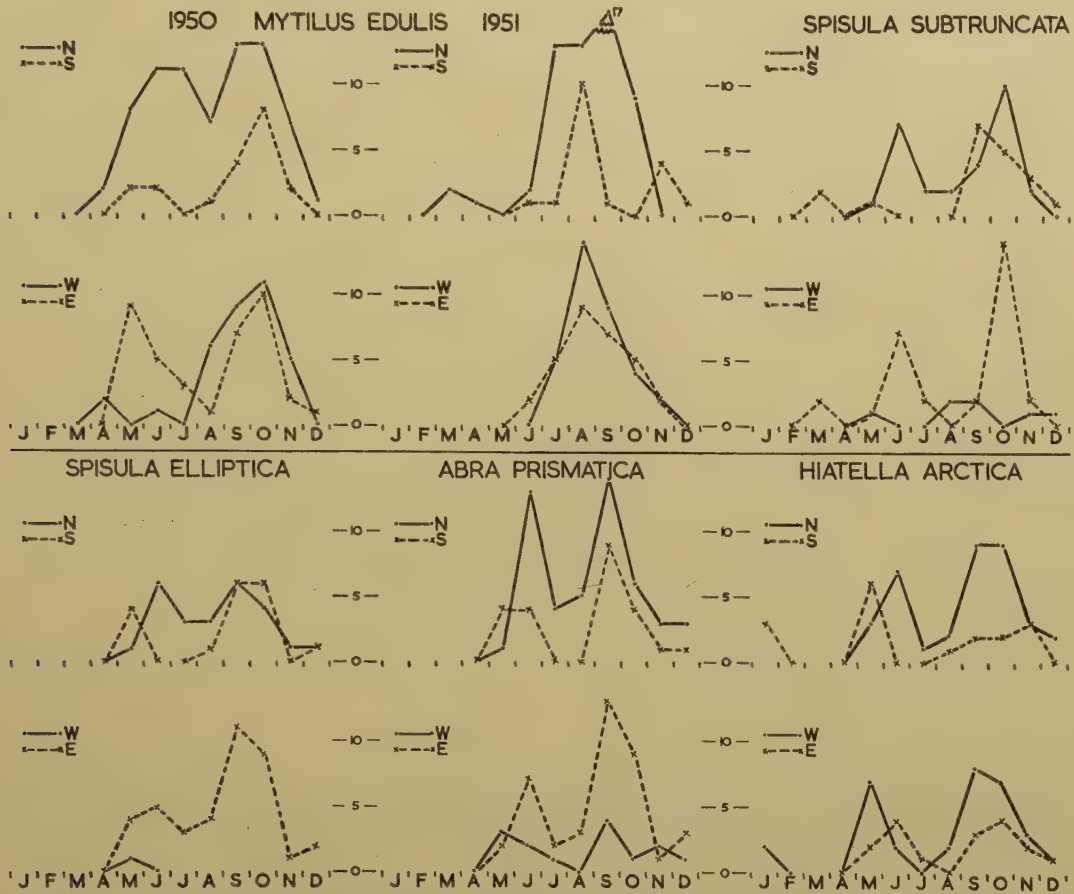
TEXT-FIG. 5.—Charts showing the distribution of samples containing 50 or more larvae of various forms in the Hensen net collections taken for the Scottish Home Department, Marine Laboratory, Aberdeen, during 1950.

so that what were two distinct periods are joined into one in the method of presentation,¹ and on the other hand to the relative scarcity of larvae in 1951. In reconsidering 1950, the greater number of samples, compared with 1949, which contained larvae of some of the more common species allows a subdivision of the North Sea so that the geographical factor may be partially eliminated. It is, of course, possible that a species may breed at different times in the north and south, so that the combination of the results may give the appearance of a double breeding, or, for that matter, continuous breeding. This point was not specially raised in the first report but a cross check between the table and the charts does not support this possibility.

Text-fig. 6 shows, for various species, the numbers of samples containing the species in each month in four subdivisions of the North Sea: north and south of a line from Newcastle to the Skaw (north; south) and the combined western

¹ If the number of samples containing larvae in successive months is 1, 9, 3, 1, 9 the same symbol (+) is used for each month though there are two distinct maxima.

halves (west) and eastern halves (east) of the Leith- and Hull-Copenhagen routes. Almost every curve may be interpreted most easily as bimodal. This is true not only for species previously recognized as showing this feature (the *Spisula spp.*) but also for *Abra prismatica* and *Hiatella arctica*, which were previously accepted as



TEXT-FIG. 6.—Graphs giving the number of 10-mile samples containing larvae of various species in each month of 1950 (also 1951 of *Mytilus edulis*) in four sub-divisions of the North Sea. The sub-divisions are north and south of a line Newcastle to Skaw and east and west of the central North Sea.

single, autumn breeders (Table I in Rees, 1951). There is, at least, no evidence here that the geographical factor is involved.

This feature of the apparent double breeding, in the course of the year, of some species has already been discussed (Rees, 1951, p. 124). The three years results suggest that the phenomenon is not restricted to a distinct set of species and it may be further tentatively suggested that the feature is related to the Atlantic influx into the North Sea and the reciprocal influx through the Dover Straits.

TABLE I.—*The Number of 10-mile Samples in which Larvae were Observed in Each Month of 1950 and 1951.*

		J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
(a)																									
Ensis ..	..	..	..	..	+	*	●	●	+	+	..	..	+	+	..	+	+	+	+	..	..	..	..	..	..
Mya truncata..	..	..	..	..	+	*	+	..	..	..	..	..	..	..	..	..	+	+	..	..	..	..	..	..	..
Zirfaea crispata	..	..	+	..	+	+	*	+	+	..	..	+	+	+	..	..	+	+	+	+	+	+	..	..	..
(b)																									
"Montacuta"	..	..	..	..	..	..	+	*	+	*	+	..	+	..	..	..	..	..	..	+	*	+	..	+	..
Cardium A ..	..	..	..	..	..	..	+	+	..	+	..	..	..	..	..	..	..	..	+	..	+	..	..	..	..
Hiatella gallicana	..	..	..	..	..	+	+	*	+	..	..	+	..	..	..	..	..	+	+	+	+	+	..	..	..
(c)																									
Modiolus modiolus	..	..	..	..	..	..	+	..	+	+	+	*	+	+	+	..	+	+	..	..	..	+	+	+	+
Hiatella arctica	..	..	+	..	..	..	+	+	+	+	*	*	+	+	+	..	..	..	..	+	*	*	+	+	..
(d)																									
Mactra corallina	..	..	..	..	..	+	+	+	..	..	+	..	..	..	..	..	..	..	..	+	+	+	+	..	..
Mactrid E ..	..	..	..	..	..	+	+	+	..	+	..	..	..	..	..	..	..	..	..	..	..	..	+	..	..
(e)																									
Mytilus edulis	..	..	..	..	..	+	*	*	*	+	*	●	+	+	..	+	+	..	+	*	■	*	+	+	+
Cardium B ..	..	..	..	..	..	+	+	..	+	..	+	+	+	..	..	..	..	..	..	..	+	+	+	+	..
(f)																									
Modiolus phaseolinus	..	..	..	..	..	..	..	*	*	+	+	+	+	..	+	..	+	+	+	+	+	+	..	..	..
Spisula subtruncata ..	..	..	..	..	..	..	+	+	+	+	*	*	+	+	+	..	..	..	..	..	..	+	+	+	..
Spisula elliptica	..	..	..	..	..	..	+	+	+	+	*	*	+	+	..	+	..	..	+	..	+	+	..	+	..

1950.

1951.

+ = 1-9 samples ; * = 10-19 samples ; ● = 20-29 samples.

The Atlantic influx in the north occurs, commonly, in two main pulses, in spring and in autumn (Tait, 1937).

Notes on Species.

A few species were obtained so infrequently that it is not worth publishing charts to illustrate their distributions. The following notes concern these species.

MYTILID B.—This was found once only, off the Skagerrak in June, 1951.

MYTILID C.—This was found once in 1950, near the West Dogger in May. In 1951 it was obtained in the Skagerrak in three samples in July and in two in August.

Cyprina islandica.—This was found in 1950 only, in one or two samples towards the east of the Dogger Bank in March and September.

Spisula solida.—In 1950 this was found only on the Hull-Rotterdam line, in June and October. In 1951 an empty shell was obtained in a sample taken off the Skaw.

(? *Tellina pygmaea*).—This was found only in September, 1951, in two samples off the Skaw and one in the Heligoland Bight.

(? *Donax vittatus*).—This was found only in September, 1950, in the Heligoland Bight.

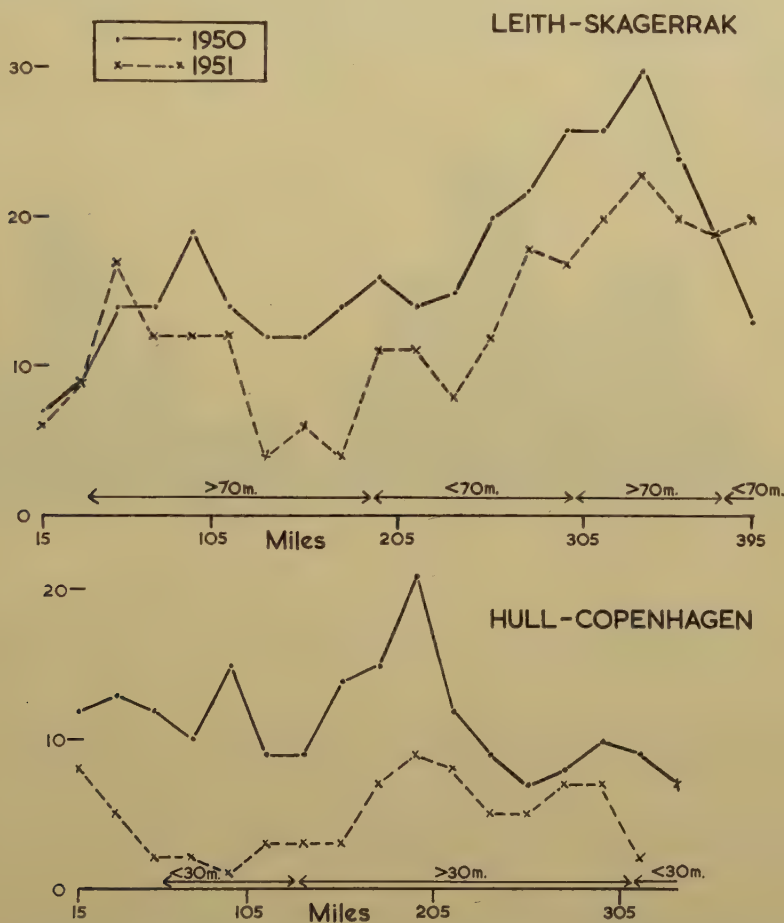
Teredo navalis.—Larvae were found in one sample in the southern North Sea in September, 1950, and in one off the Skagerrak in October, 1950.

Thracia A.—This was obtained off the Skaw in October, 1950, and in the Heligoland Bight in 1951.

Thracia B.—This newly-described larva was found off the Humber in May, 1950.

DISCUSSION.

Text-fig. 7 corresponds to Text-fig. 5 of the first report (Rees, 1951, p. 122) and shows the number of species found in each block analysed throughout each year on the Leith-and Hull-Copenhagen routes ; depths along the routes are broadly indicated. On both routes there was a marked reduction in the variety of species in 1951 compared with 1950.



TEXT-FIG. 7.—Graphs giving the numbers of species obtained in the 10-mile samples along the Leith-Skagerrak and Hull-Copenhagen routes in 1950 and 1951. Depths along the routes are broadly indicated. This text-figure corresponds to Text-fig. 5 of Rees (1951).

The spatial trend in the two years on the Leith-Skagerrak route was very similar ; the greatest variety occurred at the same position, 335 miles from the Forth, and the lowest at about 140 miles from the Forth. The 1950-51 trends were, however, markedly different from that of 1949 from about 195 miles from the Forth eastwards, although to the west of this point all three years agreed. An

association between depth and number of species was suggested in 1949 (Rees, 1951, p. 123); this was not maintained in 1950-51.

The trend on the Hull-Copenhagen route in each year was also similar, the greatest variety occurring at the same position, 195 miles from the western end. This is just over the south-eastern edge of the Dogger Bank in the region that heavy larval concentrations have previously been found (see Text-fig. 2 of Rees, 1951). Again, the 1950-51 trends depart markedly from that of 1949 and here also the association between depth and number of species, suggested in 1949, was not maintained.



TEXT-FIG. 8.—Histograms giving the number of species obtained in each month of 1950 and 1951, taking in all Recorder samples from the North Sea. This text-figure corresponds to Text-fig. 6 of Rees (1951).

The number of species obtained in each month over the whole North Sea is shown in Text-fig. 8, corresponding to Text-fig. 6 in Rees, 1951, p. 123. The trends in all three years are in general agreement. The dip in October, 1951, in the diagram probably has no ecological significance; it might well be due to reduced sampling in that month.

A list was given in the first report (p. 125) of the 10 most abundant larvae. This list is incorporated in Table II here, which gives the approximate number of hundreds of larvae of the most abundant species in each year, and the yearly averages for 1949-51. The species are placed in descending order of yearly averages. An estimate of total larvae is also given. The letters N and S have been used to indicate those forms in which at least three-quarters of the larvae were obtained north or south of a line from Newcastle to the Skaw.

The numbers in this table must be taken with some reserve. The larval populations can change rapidly so that dates of sampling and the extent of sampling both have a substantial effect on the numbers obtained. A typical example is

TABLE II.—Giving, in Hundreds, the Numbers of Larvae of Various Forms Obtained in Each Year 1949 to 1951, and the Average of the Three Years. N stands for North, S for South as Explained in the Text.

	Average. 1949-51.	1949.	1950.	1951.
<i>Mytilus edulis</i>	173N	18	210N	292N
<i>Spisula elliptica</i>	52S	140S	13	3
<i>Ensis</i>	46	22S	110	4S
<i>Abra prismatica</i>	24N	21	41N	11
<i>Cultellus pellucidus</i>	19	26S	25N	6
<i>Glycymeris glycymeris</i>	17	20N	20	11
<i>Montacuta ferruginosa</i>	17S	17S	22S	11
<i>Zirfaea crispata</i>	15S	23S	21	1
<i>Modiolus modiolus</i>	11N	13N	11N	10N
<i>Spisula subtruncata</i>	9	9S	17	3
<i>Mya truncata</i>	9	1S	26	+
<i>Venus D</i>	9N	+	26N	+
<i>Hiatella arctica</i>	8N	11N	10N	4N
<i>Abra nitida</i>	7	3	12	5
Other species	56	65	62	42
Total larvae	472	388	627	405N

the low number of *Mytilus* in 1949. It is possible that this number would have greatly increased if the first 80 miles off the Forth in August and September had been sampled. Nevertheless, the table shows many points of interest.

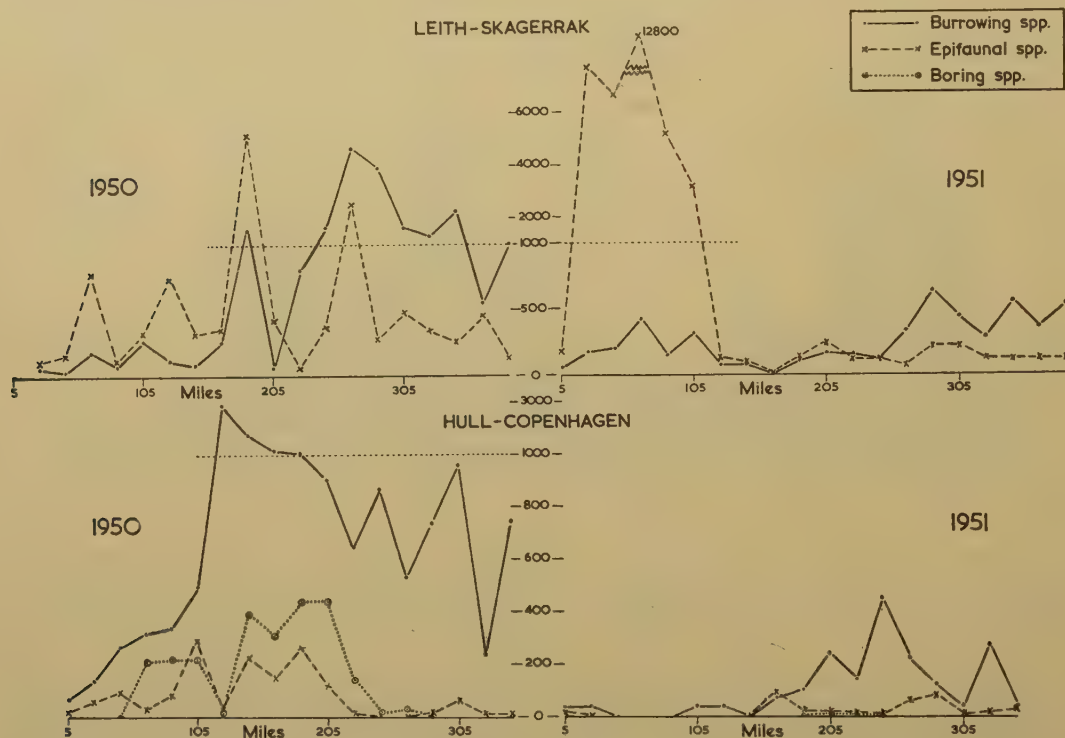
An outstanding feature is the marked predominance of *Mytilus edulis* which, overall, was more than three times as common as any other species. Since it was almost entirely northern in its distribution, the quantity of "total larvae" in the north was substantially greater than in the south. Forms more common in the south than in the north were *Spisula elliptica*, *Ensis*, *Montacuta ferruginosa*, *Zirfaea* and *Abra nitida*.

In several respects the years were very different. Despite the much lower total number of larvae in 1949 compared with 1950, several species were obtained in almost identical numbers: *Cultellus*, *Glycymeris*, *Zirfaea*, *M. modiolus*. The very great success of *Spisula elliptica* was, however, limited to 1949.

Apart from *Mytilus* larvae, the year 1950 was especially noted for the relative abundance of *Ensis*, *Mya truncata* and *Venus D*, all three occurring in spring and early summer. *Spisula subtruncata* was nearly twice as common as in 1949 and 73% were found towards the north, compared with 17% only in 1949. The relative success of *Abra nitida* in 1950 is partly accounted for by the fact that the Heligoland Bight was more thoroughly sampled than in 1949.

1951 was a poor year for larvae as a whole, even the very great number of *Mytilus* failing adequately to balance the scarcity of other species. Species notably scarce were *Spisula elliptica*, *Ensis*, *Cultellus* and *Zirfaea*.

As in the first report (Rees, 1951, Text-fig. 7), all the larvae on the Leith- and Hull-Copenhagen routes have been separated into three groups, those belonging to the burrowing, boring and epifaunal species. Text-fig. 9 shows the total number of larvae of each group in each sample of these two routes.



TEXT-FIG. 9.—Graphs giving, for 1950 and 1951, the total numbers of larvae of epifaunal, burrowing and boring species obtained in the 10-mile samples along the Leith-Skagerrak and Hull-Copenhagen routes. The vertical scale alters at 1000 larvae and a second base line (dotted) is drawn at this level. This text-figure corresponds to Text-fig. 7 of Rees (1951).

These graphs confirm the suppositions expressed in the first report that larvae of epifaunal species probably constitute a very substantial part of any pronounced concentration over the Great Fisher Bank (Leith-Skagerrak route, 1950), and that larvae of *Ensis*, a burrowing genus, may form a considerable part of the population in spring and early summer along the southern edge of the Dogger (Hull-Copenhagen route, 1950). The graphs for the Leith-Skagerrak route in 1951 reveal the tremendous dominance of the larvae of epifaunal species in the concentration off the Forth.

The main concentrations found in 1949 were briefly considered in the first report and the specific composition of the concentrations indicated. Most of the main concentrations obtained in 1950 and 1951 have been numbered in Text-fig. 1, and the percentage composition of these numbered patches given in Table III: only the dominant species are included.

TABLE III.—*Giving the Percentage Composition of Patches of Larvae in 1950 and 1951. The Patches are shown and numbered in Text-fig. 1.*

Patch.	Month.	<i>Mytilus</i>	<i>M. modiolus.</i>	<i>Mytilid A.</i>	<i>A. prismatica.</i>	<i>Ensis.</i>	<i>Cultellus.</i>	<i>Zirfaea.</i>
1950.								
1*	IV	—	—	—	—	72	—	—
2	V	4	2	—	—	74	1	10
3	V	82	—	—	2	—	—	4
4	V	73	—	—	—	10	—	—
5	V	—	—	—	—	89	—	2
6*	VI	—	—	3	20	14	5	—
7	VI	13	—	20	20	27	—	20
8	VI	—	—	—	—	80	—	20
9	VII	94	—	6	—	—	—	—
10	IX	6	78	—	2	—	—	—
11*	IX	74	5	2	4	—	—	—
12*	IX	—	—	—	35	—	45	—
13*	IX	5	—	—	35	—	29	—
14*	IX	—	—	—	1	—	1	—
1951.								
1*	VI	—	—	—	26	9	5	—
2	VIII	99	+	+	+	—	+	—
3	IX	55	37	—	—	—	—	—

* Also in 1950, Patch 1, *Macra corallina* 18%; Patch 6, *Spisula subtruncata* 10%, *Venus* D 28%; Patch 11, *Glycymeris* 9%; Patch 12, *Cardium* D 10%; Patch 13, *Spisula elliptica* 8%; Patch 14, *Abra nitida* 63%, *Montacuta ferruginosa* 24%; in 1951, Patch 1, *Macra corallina* 45%.

A brief account has recently been given of a resurvey, in 1950 and 1951, of the bottom fauna of the Dogger Bank (Ursin, 1952). Birkett (1953) has commented on this account and, in the main, confirmed the findings of Ursin. The available results on the bottom fauna are, however, as yet too meagre and from too restricted an area to allow any useful comparison between larval distribution and the contemporary bottom fauna. It would seem, from the larval results, that it is important to establish the age composition of the bottom fauna, to establish, in fact, whether there are dominant year classes. There can be very great differences in the numbers of larvae obtained from year to year, differences which may be reflected in the bottom fauna. As examples, we can note the great number of larvae of *Spisula elliptica* in 1949, of *Ensis* and *Mya truncata* in 1950, and the scarcity of larvae of *Cultellus* and *Zirfaea* in 1951 (Table II).

Distribution of Mytilus edulis larvae.—A question which arises is whether the Fisher Bank concentration of 1950 and the Forth concentration of 1951 were made

up of larvae which had originated *in situ* or whether larvae had been carried to these regions; and if carried, from which direction had they come? The concentrations as a whole consist of heterogeneous assemblages of species, but the distributions of the larvae of *Mytilus edulis* hold particular interest, partly because these larvae played a dominant part in both concentrations and partly because of the distribution of adult mussels, which, on the evidence, is closely restricted to coastal waters.

Schrader (1911) referred to *Mytilus edulis* as a coastal form. He did find a young specimen as deep as 42 m. but assumed that this must have developed from a larva which had been carried from the coast. He pointed out that the species occurs down to a depth of 20 m. off the Norwegian coast. The general absence of mussels in Schrader's North Sea samples cannot be explained by unsatisfactory means of collecting, for other epifaunal species were found in numerous samples.

At first sight it might seem that the grab surveys of Davis (1923, 1925) and Stephen (1933) are not really relevant to the question of the distribution of adult *Mytilus* in the North Sea. This, however, is not so. The mussel community shows its greatest development, not on rocky ground, but in sand and mud regions (Remane, 1940), that is, on bottoms such as are sampled by the grab. Davis (1925) did find *Mytilus* at one station, in 35 m. of water but less than three miles from the coast.¹ The grab is, in fact, capable of taking samples of *Mytilus*. At about 200 grab-stations, Petersen (1914) found *Mytilus* at 18% of the stations and the horse mussel, *Modiolus modiolus*, at another 7%. Excluding the half-dozen stations taken in the "true Baltic," where conditions cause an unusual distribution of animal communities, Petersen obtained *Mytilus* in 50% of the stations less than 14 m. in depth. The deepest station where *Mytilus* was found was 18 m. We may, therefore, accept the absence of *Mytilus* in the offshore samples taken during the grab surveys of the North Sea as evidence of its scarcity or absence in this region.

Hargreaves (1910) compiled a long list of lamellibranch species which had been recorded on the Dogger Bank. *Mytilus* was not included in this list.

White (1937) gives the usual habitat as from high water mark to a few fathoms. Jensen (1912) said that it belongs to the littoral belt.² He found young specimens at greater depths, down to about 100 m., but considered that such specimens must have been carried out into deep water with seaweed. In the western Atlantic it is said that mussels live down to a depth of about 30 m. (Anon., 1952).

Verwey (1952) states that the mussel is usually limited to shallow water, down to a depth of 6-9 m.; exceptionally, however, large banks may occur in somewhat deeper water of up to 17 m. or more. In the North Sea, at some distance from the coast, mussels are absent except near the surface, on buoys or lightships.

These results, as well as those of many other workers, show that we can discount

¹ Dr. A. C. Stephen has very kindly looked through his records and checked that he found no *Mytilus*, either living or as empty shells, at a greater distance than two miles from the coast.

² The term "littoral" is variously used, but it is implicit elsewhere in his report that Jensen did not consider a depth of 13 f. to be in the littoral region.

the possibility that adult *Mytilus edulis* occur in appreciable numbers, if at all, in depths greater than 40 m. in the North Sea, or, in shallower water, on the Dogger Bank. The 20 m. and 40 m. depths contours are shown in Text-fig. 12 and it is clear from these that we may regard the occurrence of appreciable numbers of mussels as limited to a few miles off the coasts.

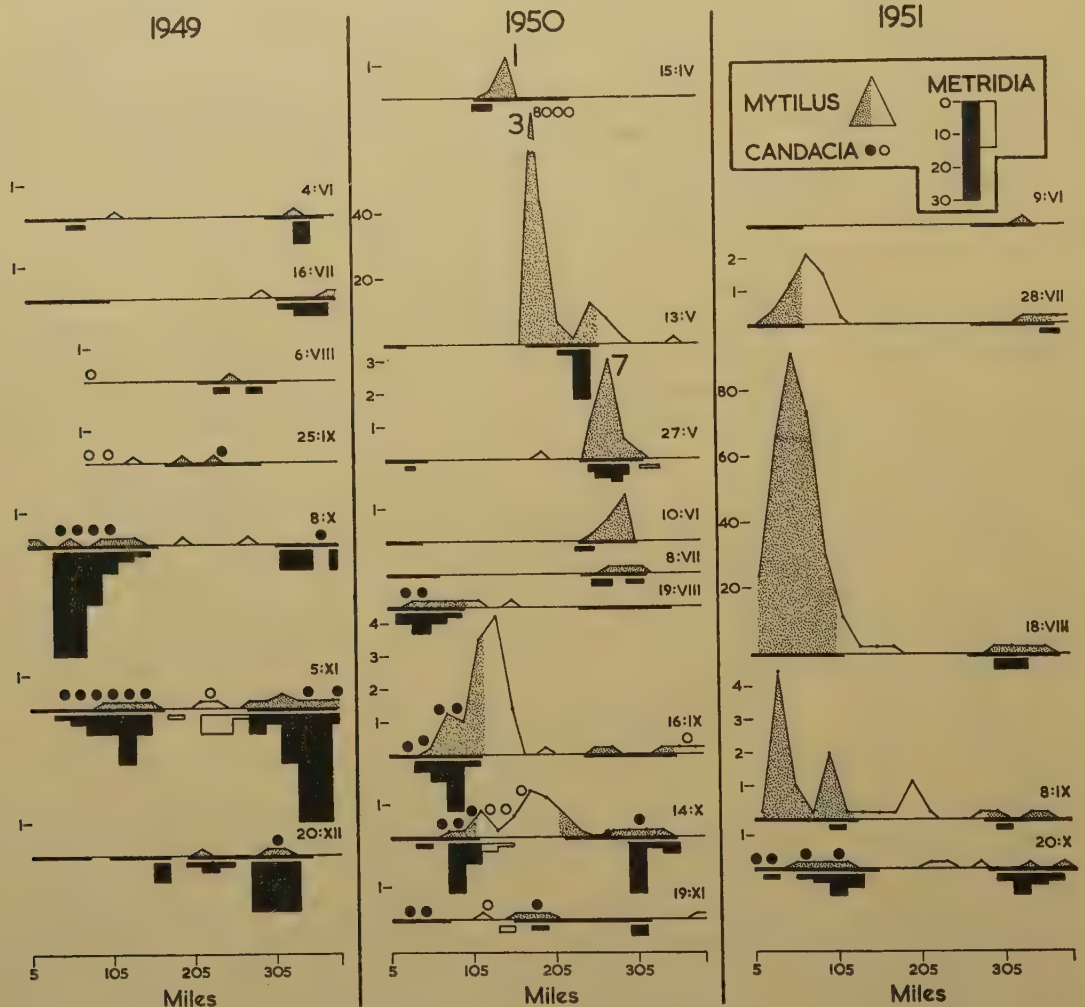
A preliminary scrutiny of the distribution of *Mytilus* larvae gives a partial answer to our question of origin. It can be seen on Plate VII that a very heavy concentration of *Mytilus* larvae was obtained in the centre of the North Sea in May, 1950. This particular concentration, of about 3000 larvae per m³, was found to compare favourably with high population densities of lamellibranch larvae obtained elsewhere and by other methods of collecting (Rees, 1951, p. 108). These *Mytilus* larvae were large and must have been several weeks old. There can be little doubt that these old larvae, in such a great concentration, must have originated in inshore waters where *Mytilus edulis* occurs in dense colonies.

An apparent association between *Clione*, which is regarded as an indicator of north-west North Sea water (Marshall, 1948), and high larval lamellibranch concentrations over the Great Fisher Bank was referred to in the first report (Rees, 1951, p. 129). Also, several examples were given (p. 127) of larvae which appeared to show a southwards movement during the autumn, at a time when it is usual for north-western indicator species to show a similar southwards progression. We should, therefore, attempt to relate the distributions of *Mytilus* larvae, which are taken to typify the two major concentrations, to the north-western North Sea indicator species. Of these, the copepod *Metridia lucens* is, at present, the most suitable for the purpose, partly because it is relatively abundant and persistent, much more so than *Clione*, for example, and partly because its distribution in the years under review is readily available from the results of the routine analysis of the plankton. Although much less numerous, the distribution of *Candacia armata* closely resembles that of *Metridia lucens* in the North Sea (Rae and Rees, 1947).

Text-fig. 10 shows (above the line) graphs of the distribution of *Mytilus* on each Leith-Skagerrak record which contained appreciable numbers of the larvae. Underneath the base line, which represents the record, are placed histograms of the numbers of *Metridia lucens* found on each 10-mile sample analysed and, above the base line, circles mark the samples containing *Candacia armata*. There is a remarkably good agreement between the distribution of *Mytilus* and *Metridia*. 1950 provides the best series. Patches of *Metridia* and *Mytilus* overlapped or coincided from April to July and, from an easterly position of coincident patches in July, a switch over to the west was shown in both species on the August record. From August to November both species showed an easterly trend along the line. *Candacia* also occurred in the association from August onwards and also showed the easterly trend.

In 1951 the agreement between *Metridia* and *Mytilus* is again well shown in the easterly patch from July to October. *Mytilus* appeared suddenly in the west,

off the Forth, in late July but *Metridia* was not recorded with it until September and, even then, only one specimen was found. *Candacia* was not obtained until October. On the whole, the occurrence of *Mytilus* larvae off the Forth in 1951 conformed to the distribution of *Metridia* most commonly found. *Metridia* and/or *Candacia* were first found off the Forth, after a summer absence, in August 1946, 1948, 1949 and 1950 but not until later than August in 1938 and 1947. In 1949



TEXT-FIG. 10.—Graphs and histograms giving the number of larvae of *Mytilus edulis* and of the copepod *Metridia lucens* in each 10-mile sample of a series of Leith-Skagerrak records in three years. The samples containing *Candacia armata* are indicated by circles. Each base line represents a Leith-Skagerrak line in its full length from the Forth to the Skagerrak and the thickened parts of each base line show the sections of the record which sampled between sunset and sunrise. The dotted parts of the graphs for *Mytilus* and the black histograms for *Metridia* show specimens taken during sampling at night. The vertical scale to the graphs is in hundreds of larvae. See footnote p. 23.

there was a reasonably close agreement between *Mytilus*, *Metridia* and *Candacia* on the eastern side, but, unfortunately the information was lacking at the western end of the route in August and September.

The similarity between the two distributions is close. It may therefore be said that the *Mytilus* larvae whose distributions are shown in Text-fig. 10 were contained in water inhabited by *Metridia lucens*. It was clear from our pre-war results that *M. lucens* is an indicator of mixed oceanic and coastal water, "elegans" water, in the North Sea (Rae and Rees, 1947), and this has been fully confirmed by the post-war results (Rae, 1949-52). It appears, then, that *Mytilus* larvae which occur off-shore in the northern North Sea (Text-fig. 10) are to be found in mixed water. It is, of course, obvious that we cannot generalize from this and say that *Mytilus* larvae are everywhere to be found only in mixed oceanic and coastal water. The fact that the adult is essentially a coastal and very shallow water form clearly precludes any such generalization.

Supplementary records were taken in May, 1950, besides the normal routine records. The records which now concern us are shown in the chart on the left of Text-fig. 11. In addition to Recorder samples, there were the Hensen net samples taken by the research vessels of the Marine Laboratory, Aberdeen. Consideration of the distribution of *Mytilus* larvae during this period requires that particular attention is given to the dates of sampling; these are given in the chart in Text-fig. 11.

No *Mytilus* larvae were found on the Aberdeen-Lerwick (A) and 12 TA records. The distributions on the three Leith-Skagerrak (K) records are given in Text-fig. 10. The distribution on the 7 TB record is shown in Text-fig. 11, the north leg and south leg being given in separate graphs; it also shows the distribution of larvae on the eastern half of the Hull-Copenhagen (C) record.

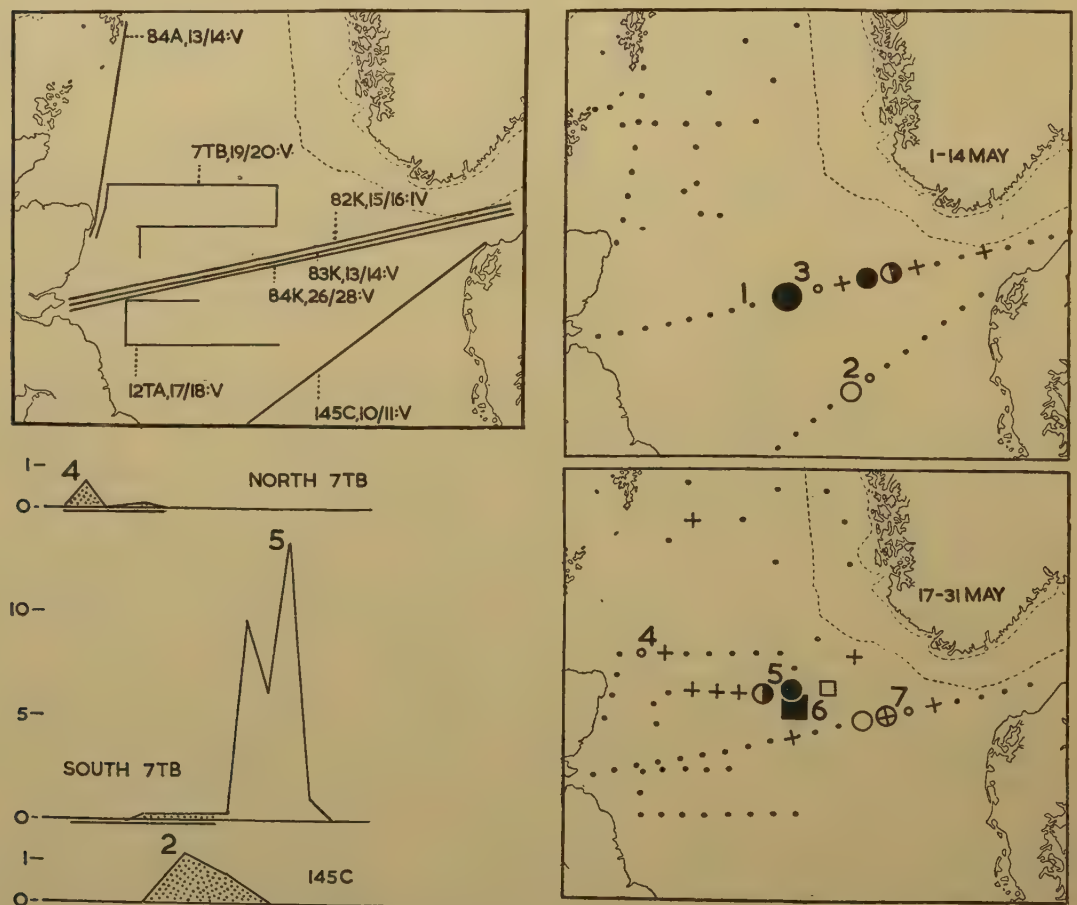
Charts showing the number of *Mytilus* larvae in each sample, Recorder and net, are given in Text-fig. 11, one chart for the period 1-14 May and the other 17-31 May. The samples containing the greatest number of larvae in each graph have been numbered (Text-figs. 10 and 11) and the numbers transferred to the charts. The numbers are more or less in date sequence: 2, May 10th; 3, May 13th; 4, May 21st; 5, May 20th; 6, May 24th; 7, May 27th. In addition, the concentration numbered 1 (April 15th record in Text-fig. 10) appears to be relevant to the distributions we are considering and the geographical position of this is shown in the chart for 1-14 May.

The symbol numbered 6 in the chart for 17-31 May in Text-fig. 11 refers to a Hensen net sample. This was an exceptional sample for it contained twice as many total larvae as any other net sample taken throughout the year. The measurements of one hundred *Mytilus* larvae from this net sample fell into the range 360-470 μ with an average of 413 μ . All the larvae were, in fact, very large, larger than the normal settlement size. They must have been several weeks old, sufficiently old to have allowed transportation over a considerable distance.

It is clear from the charts, that the axis of highest concentrations found on

records and Hensen net samples lies in the general direction WNW.-ESE. Since sampling took place irregularly over a relatively long period, any expectation that the numbers obtained would decrease with increasing distance from the source could hardly be realized.

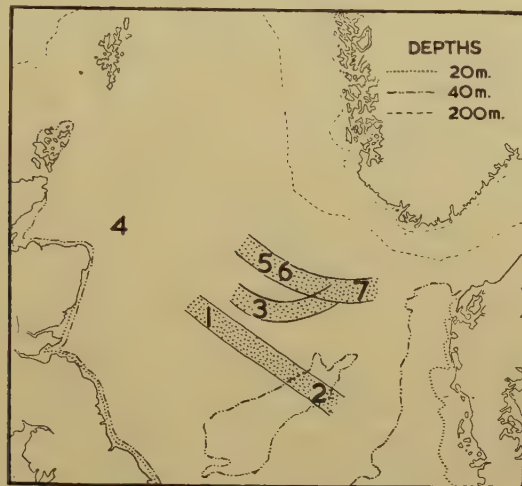
The concentrations found on the Recorder routes were relatively narrow in their west-east axes (Text-fig. 10 and 11). The implication is that the distributions were narrow and elongated, that is, they took a form which we can, for convenience, refer to as "band" distributions. A schematic representation of this feature is shown in Text-fig. 12 where boundary lines are drawn to enclose samples containing



TEXT-FIG. 11.—The chart at the top left shows the routes and dates of records taken in May, 1950. The charts on the right show the distribution of *Mytilus* larvae in Recorder and net samples in the periods May 1st–14th and May 17th–31st; the scale for the symbols is as shown in Text-fig. 13. The three graphs show the number of *Mytilus* larvae in samples along sections of records, the vertical scale being in hundreds of larvae. Peaks in these three graphs, and in the appropriate records in Text-fig. 10, have been numbered and the location of the peaks shown by similar numbers in the two charts on the right. See footnote p. 23.

appreciable numbers of larvae. It is not suggested that Text-fig. 12 is an accurate representation of the positions of the bands; one cannot allow for the distribution changing in association with the successive times of sampling. Other, perhaps equally acceptable, ways of representation could be chosen but they would present essentially the same features of long, narrow distributions.

Such features accord well with the accepted idea of the water circulation of the North Sea at this season, and cannot fail to remind one of the stream currents described by Tait (1937). However, we cannot conclude from this evidence alone that the incoming water was confined to narrow streams. Given a continuous spawning of *Mytilus*, an elongated distribution of larvae might form near the



TEXT-FIG. 12.—The suggested distributions of *Mytilus* larvae in the spring of 1950.

edge, say the western one, of a much wider inflow of water. The water carrying the larvae must, however, have moved comparatively rapidly to have carried larvae some hundreds of miles during their period of pelagic life.

Even without the extra samples which have suggested such a picture as Text-fig. 12, there is strong circumstantial evidence of the *Mytilus* larvae being distributed in narrow bands. On five successive Leith-Skagerrak records between April 15th, and July 8th, 1950, there were patches of *Mytilus* larvae restricted to a distance of about 30 or 40 miles in their east-west axes (Text-fig. 10). One cannot accept the premise that these five records sampled the same population; a generous estimate of the larval life of *Mytilus* is five weeks (Chipperfield, 1953) and, in fact, the larvae taken even in the earliest record, April 15th, were already large and in the later stages of pelagic life. One must, therefore, postulate a more or less continuous recruitment of larvae in the region of the Great Fisher Bank over a period of some three months. Since these larvae must have originated in shallow waters it is only reasonable to conclude that these shallow waters were to the north and

west, in view of the accepted idea of circulation in the North Sea (Tait, 1937). The picture, therefore, is of a distribution of *Mytilus* larvae some 200–300 miles long in its NW.–SE. axis but only 30–40 miles in its E.–W. axis, that is, a “band” distribution.

It seems, then, that the *Mytilus* larvae in the central North Sea in May, 1950, originated off the north British coast (including, possibly, the Orkneys and Shetlands), at least 200 miles away. The similarity in distribution between *Metridia lucens* and *Mytilus* larvae, which was particularly close in 1950 (Text-fig. 10), strongly suggests that the band distribution of *Mytilus* was, in some way, due to the movement of mixed Atlantic and North Sea water.

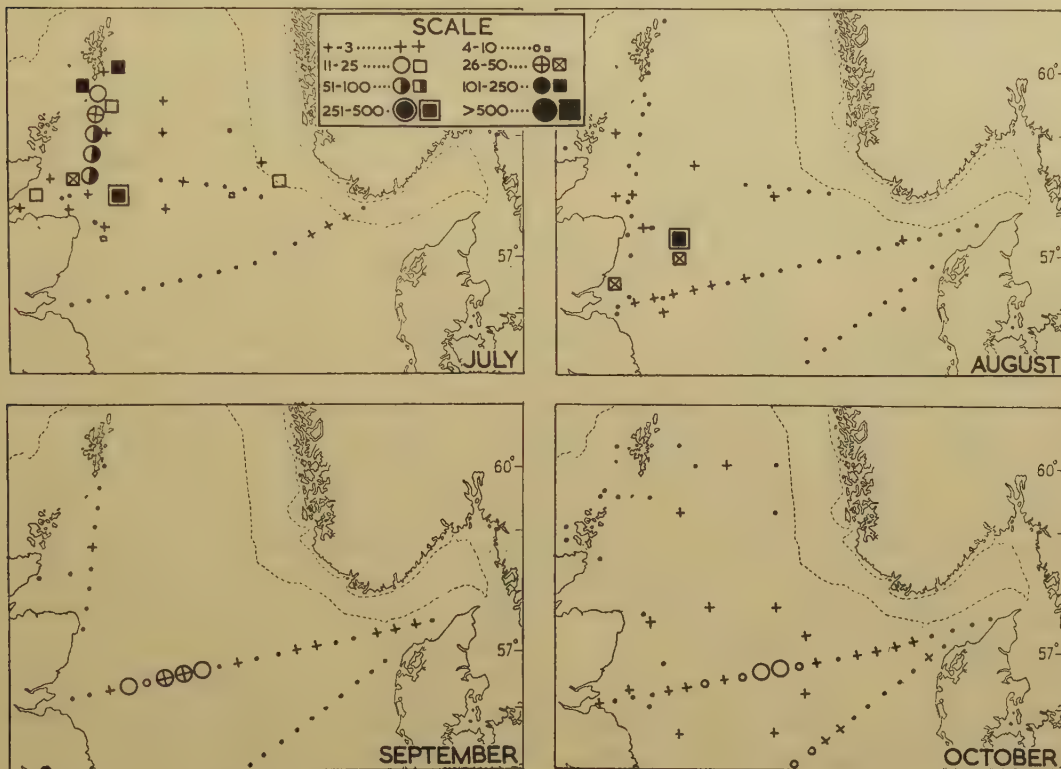
As regards the occurrence of an exceedingly heavy concentration of *Mytilus* larvae off the Forth in August, 1951, the only information available is given in the charts of distribution in Plate VII. It is, of course, inherently likely that these larvae had also been carried southwards in mixed water which had come from the north-west North Sea. More often than not, the indicator species of such mixed water re-appear off the Forth in August; the way *Metridia lucens* illustrates this feature is noted on p. 38. Although, in 1951, *M. lucens* was not observed off the Forth until September 7th, the high numbers of *Calanus finmarchicus* and *Limacina retroversa* here in mid-August indicated that mixed water had, in fact, reached the area from the north.

It must be recognized that some, at least, of the larvae originating from the numerous *Mytilus* colonies in the Forth are, doubtless, carried into the North Sea. On the evidence of the indicator species, one would expect the larvae of August and September to be carried in a southerly or south-easterly direction. It is very unlikely that many larvae would be transported, at this season, for any appreciable distance directly eastwards, that is, along the Leith-Skagerrak route. Even in August, 1951, when a Forth origin may most readily be suspected, the greatest population density of larvae was found 60–70 miles east of the entrance to the Forth and very large numbers were found up to 100 miles eastwards (Plate VII, Text-fig. 10). In fact, it is most likely that these larvae came from the north in the southerly or south-easterly drift.

A partial demonstration of an actual southwards drift is given by the distribution of *Mytilus* larvae in July–October, 1950, using the Hensen net samples as well as Recorder samples (Text-fig. 13). *Mytilus* larvae were very abundant in the north-west in July and became scarce in August. Larvae were absent off the Forth in July and a moderate concentration was found some distance east of the Forth in September and still further east in October. Appreciable numbers were found east of the Dogger Bank, on the Hull-Copenhagen route, in October.

It is worth while looking more closely at Text-fig. 13 with the distributions of the previous May in mind. The patches on the Leith-Skagerrak routes of September 16th and October 14th may reasonably be compared with the concentrations numbered 1 and 3 in Text-fig. 10 and 11, and that near the Dogger Bank on October 22nd with 2 in Text-fig. 11. The same considerations apply as in the

case of May 1950 ; the *Mytilus* larvae in the centre of the North Sea must have been transported many miles from coastal waters and, because of the duration of larval life, it is very unlikely that a single concentration sampled on September 16th was re-sampled further to the east on October 14th. It would seem that we should here again postulate a continuous recruitment of larvae. The alternative is to accept the coincidence that successive Leith-Skagerrak records sampled discrete



TEXT-FIG. 13.—Charts showing the distribution of *Mytilus* larvae in each month from July to October, 1950, in Recorder samples and in Hensen net samples of the Scottish Home Department, Marine Laboratory, Aberdeen. The circular symbols stand for number per mile per 10-mile Recorder sample and the square symbols for number per net sample in tens.

patches of larvae, each patch having travelled many miles from the coast. Clearly, we do not have at this time anything like so detailed a picture as in the spring ; that region north of the Forth, which was sampled reasonably well in May, not only in number of samples but also within short intervals of time, was sampled very sparsely in the summer and autumn. There were, at best, hardly more than four or five net samples in a month over some thousands of square miles and, of particular importance, there was no suitable Recorder run to give a continuous traverse of the area. Even so, both in July and August a very large number of

larvae was found in one net sample whilst neighbouring samples had few or none, as happened also in May. There are, in fact, strong indications that in the autumn, as well as in the spring of 1950, the drift which had picked up *Mytilus* spawn in some coastal water had retained the larvae in a narrow, elongated distribution some hundreds of miles further down its course into the North Sea.

It may be as well to point out that there was a prolonged supply of large number of *Mytilus* larvae in 1950 compared with 1949 and 1951, and also with 1952 and 1953.

Since *Mytilus* larvae were dominant both in the concentration over the Great Fisher Bank in 1950 and off the Forth in 1951, it would seem, by extension of the argument, that some of the larvae of the other species in the two concentrations had also been carried in mixed water, and that these larvae originated along the route from the north-west North Sea.

The probable transport of larvae from the direction of the north-west North Sea explains the occurrence of larvae of other shallow water species, besides *Mytilus edulis*, in the central North Sea. In this connection, the distribution of the larvae of *Spisula subtruncata* may be noted (Plate VIII). The species of *Paphia*, which occurred especially in 1949, is not known but is probably a shallow water one. The estimated number of larvae of *Ensis siliqua* in 1950 was very great but there remains some doubt about the accuracy of this result (p. 27). However, it is stated in the report of the Council of the Marine Biological Association of the U.K. for 1951-52 that Mr. N. A. Holme finds that *E. siliqua* is typically a shore or shallow-water species, and *E. ensis* a typically offshore species. It is, therefore, possible that the larvae of *E. siliqua*, as well as those of *Mytilus edulis*, were unusually abundant in the central North Sea in 1950, both species being coastal forms which spawn in the spring.

Any discussion of the mechanism involved in the concentration and transport of larvae had better await the presentation of the available information on the distribution of other organisms, besides lamellibranch larvae, in May, 1950.

SUMMARY.

1. This report presents the distributions of lamellibranch larvae in the North Sea in 1950 and 1951 and follows the earlier one on the distribution in 1949 (Rees, 1951).

2. A few additional species of larvae have been described and some of the names given in the previous report have been revised (p. 25.)

3. A major concentration of larvae was found over the Great Fisher Bank in May-June, 1950. A comparison of concentrations here in four years reveals a regular form and placing of their profiles. A major concentration was found off the Forth in August, 1951.

4. In the course of a year, two main breeding periods were shown by some species.

5. The spatial trends shown by the number of species found in each sample along both the Leith-Skagerrak and Hull-Copenhagen routes were very similar in 1950 and 1951, but many more species were obtained in 1950. The trends differed from those found in 1949 and the association with depth, previously noted, was not maintained.

6. The total number of larvae of *Mytilus edulis*, obtained during 1949-51, was three times greater than the number of any other species. The numbers obtained, from year to year, of the dominant species were in several cases very different. Noted particularly were the great number of *Spisula elliptica* in 1949, of *Ensis* and *Mya truncata* in 1950 and the scarcity of *Cultellus* and *Zirfaea* in 1951.

7. Larvae of epifaunal species constituted a substantial part of the concentration over the Fisher Bank in 1950 and greatly dominated the concentration off the Forth in 1951.

8. The distributions of larvae of *Mytilus edulis* and the copepod *Metridia lucens* along the Leith-Skagerrak route were similar; the similarity was particularly close in 1950.

9. *Mytilus* larvae appear to have been distributed in narrow, elongated formations, termed "band" distributions, in May, 1950. Their cross-sections appear to have occurred in succession from west to east associated in some way, with the movement of mixed oceanic and North Sea water. The WNW.-ESE. lie of the bands indicates that *Mytilus* larvae in the central North Sea had come from the north British (including, possibly, the Orkneys and Shetlands) coast.

10. A southwards movement of *Mytilus* larvae from the north-west to the region off the Forth between July and October, 1950, is partially demonstrated.

11. The distributions of *Mytilus* larvae indicate that the concentrations of lamellibranch larvae over the Fisher Bank in 1950 and off the Forth in 1951 were due to the movement of mixed water, the larvae involved having originated along the route from the north-west North Sea.

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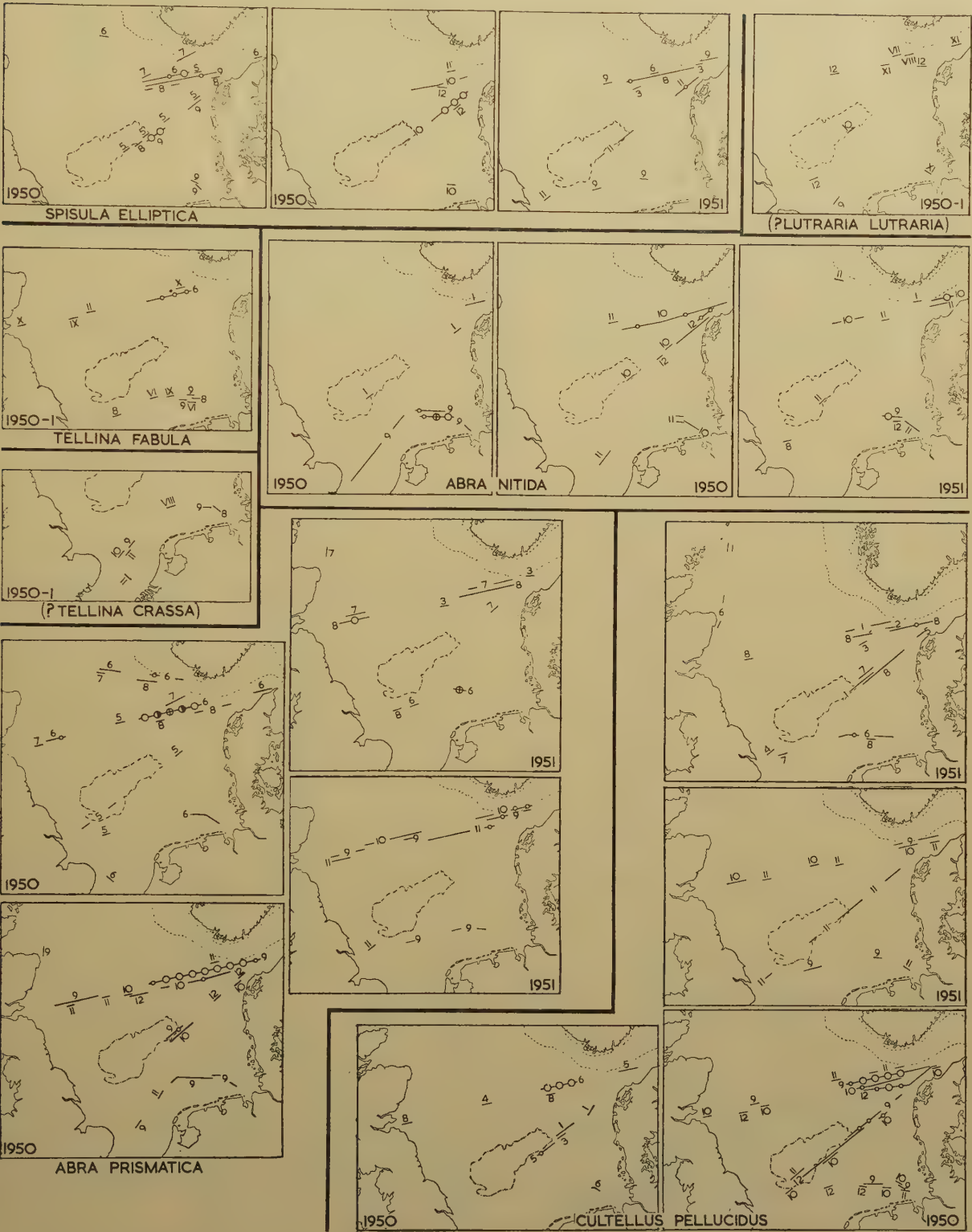
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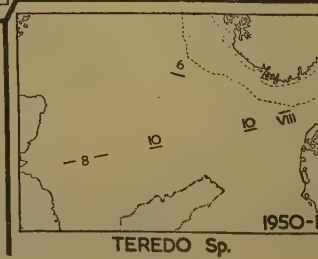
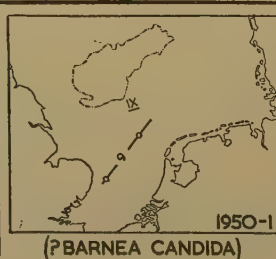
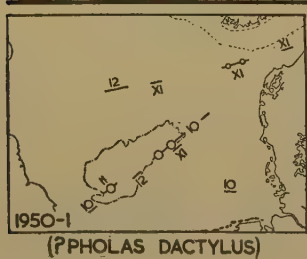
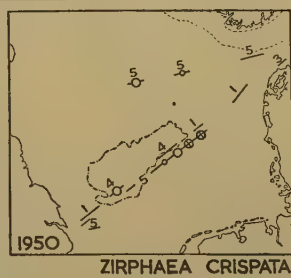
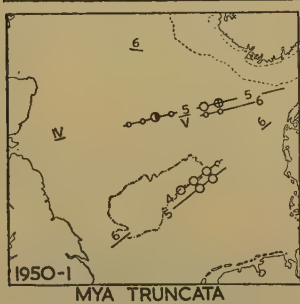
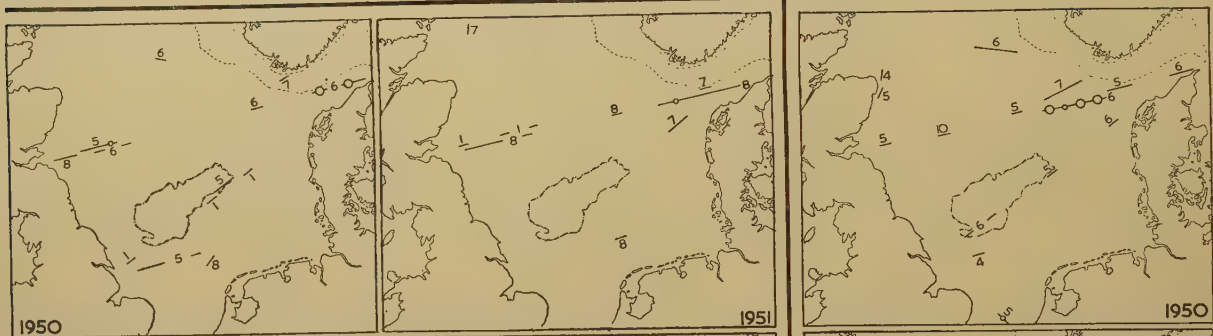
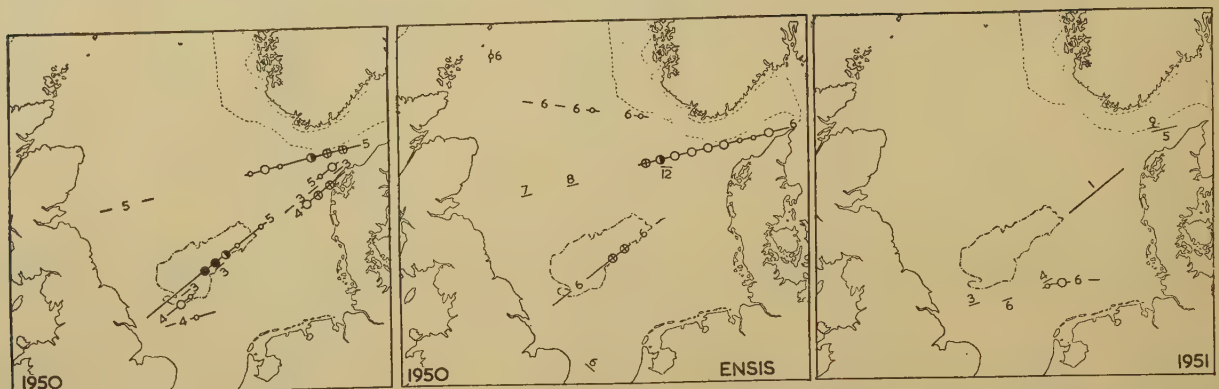
EXPLANATION OF PLATES VII-X.

Charts showing the distribution of types of larvae during 1950 and 1951. The numbers placed near the observations give the months of occurrence. When both the 1950 and 1951 distributions are shown in a single chart, the arabic numerals refer to 1950 and the roman numerals to 1951. A few of the specific names differ from those used in the charts of Rees (1951), in accordance with the revisions given on p. 25. The scale of symbols used to give broad indications of numbers is given in Plate VII.









CONTINUOUS PLANKTON RECORDS: THE DISTRIBUTION OF ECHINODERM AND OTHER LARVAE IN THE NORTH SEA, 1947-51

BY

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INTRODUCTION AND METHODS.

THIS report on echinoderm larvae is a further contribution in the general study of the distribution of the pelagic larvae of benthic animals in the North Sea, as shown by continuous plankton records. A section, placed at the end of this report, consists of a brief account of the distribution of larvae of the Polychaeta, Cirripedia, Bryozoa and Phoronidea. Earlier reports concerned the larvae of lamellibranchs and decapod crustacea (Rees, 1951, 1952, 1954).

The records obtained in each month from 1946 to 1951 are given by Rae (1952, 1953), who has also described the routine methods of plankton analysis employed. The plankton in every alternate 10-mile sample is analysed and estimates derived of the numbers of various organisms in each sample. Echinoderm larvae are at first treated as a single group and the estimate derived is not of the actual number of larvae in a sample but of the range of numbers in which the actual number lies.

For the purpose of calculation it is then assumed that the number of larvae in the sample is equivalent to the calculated mean of the range. A concrete example may be given by way of illustration. Suppose there are 4000 larvae in a sample. In routine analysis the number of larvae would be estimated to be in the range 2040–5000 larvae. In applying this estimate it is assumed that the number of larvae present is 3000, which is the calculated mean of this range. Clearly, therefore, the quantitative estimates are very approximate; continuing the example, no distinction is made between samples containing 2100 and 4900 larvae.

Whilst the identification of the echinoderm larvae is by no means so formidable a problem as that of the lamellibranch larvae, some initial difficulty was encountered because of the damaged state of the larvae on the silk. With experience, however, the identification becomes easy and all can be identified. Since it was desired to identify larvae over the same period, 1949 to 1951, as that for which lamellibranch larvae were identified, the delay in acquiring experience made it necessary to return to material that was two or three years old. So much material had accumulated that it was not possible to study the distribution of echinoderm larvae in such detail as in the case of lamellibranch larvae. For the latter, every alternate sample taken was re-examined even though none had been found in the routine analysis. For the echinoderms, only samples known to have at least a certain number of larvae were re-examined for species, the limit being placed at 480 larvae in the 1949 and 1950 material and reduced to 160 in the fresher 1951 material. In the course of re-examination of samples, only a fraction or subsample of the echinoderm larvae were identified to species. This fraction was usually about one-fortieth, which approximated to the number seen in one microscope traverse of the silk (Rae, 1952). The number of larvae of each species in a sample has then been calculated on a proportional basis.

This difference between the method used for the echinoderm and for the lamellibranch larvae should be noted, especially as it affects the scarce larvae. Since every alternate 10-mile sample was examined for species of lamellibranch larvae there was, theoretically, the same number and distribution of samples in each month. For the echinoderm larvae, however, the effective number of samples varied from month to month according to the incidence of the more abundant larvae. A scarce echinoderm larva occurring in the winter months would probably not be observed, since so few samples were re-examined during this season. On the other hand, an equally scarce larva, which occurred in the summer, might be observed several times because of the increase in the number of re-examined samples, due to the abundance of other species of larvae.

Table I gives the number of samples re-examined for echinoderm larvae in each month in two halves of the North Sea, the boundary being conveniently placed along a line Newcastle–Skaw.

Only echinoplutei and ophioplutei were estimated and identified. Larvae of the other classes of echinoderms have not been studied. Few, however, appear to have been taken in the Recorder samples.

TABLE I.—*The Number of Samples Re-examined in each Month for Species of Echinoderm Larvae.*

	Northern North Sea.				Southern North Sea.		
	1949.	1950.	1951.		1949.	1950.	1951.
February . . .	2	—	—	.	—	—	1
March . . .	—	11	5	.	—	—	—
April . . .	—	10	6	.	—	1	1
May . . .	—	15	1	.	12	6	—
June . . .	3	6	5	.	4	11	21
July . . .	—	7	6	.	23	14	15
August . . .	—	4	16	.	10	5	17
September . .	6	3	19	.	1	5	7
October . . .	3	—	3	.	—	—	3
Total . . .	14	56	61	.	50	42	65

DISTRIBUTION OF TOTAL ECHINODERM LARVAE.

The distributions of total echinoderm larvae in Recorder collections from 1932 to 1939 are given by Henderson and Marshall (1944) and Marshall (1948). In the years 1932–37 the survey was confined to the southern part of the North Sea. These distributions, as well as those in each year from 1946 to 1949, are shown in summarized form in Text-figs. 1 and 2. Similar summary distributions have been given for lamellibranch larvae (Text-figs. 1 and 2 of Rees, 1951) and decapod larvae (Text-figs. 2 and 3 of Rees, 1952).

The great majority of the samples, containing over 2000 larvae, which go to make up Text-fig. 2, were obtained during 1938–39 and, in consequence, Text-fig. 2 may represent unusual conditions which occurred in this period rather than the generalized picture for which it is intended. Whilst echinoderm larvae were very numerous in the southern North Sea in 1938–39, it is particularly to be observed that several Recorder routes converged into the Heligoland Bight. There was little sampling into the Bight in 1946–49. In 1950–51 the Bight was more thoroughly sampled, although not to the extent of 1938–39, and the distributions, which are shown in Text-fig. 3 in a form comparable with similar charts for lamellibranch larvae (Text-fig. 1 of Rees, 1954), do confirm that the greatest concentrations of echinoderm larvae in the North Sea are found in the Heligoland Bight.

There is a clear difference between the distributions of the three main groups of larvae. The main concentrations of lamellibranch larvae have been found within an arc stretching from the south-west Dogger Bank to the Great Fisher Bank and westwards to the Forth; of decapod larvae within the southern North Sea, west as well as east; and of echinoderm larvae within the eastern half of the southern North Sea and particularly within the Heligoland Bight.

Marshall's (1948) charts of distribution of echinoderm larvae in 1938 and 1939 illustrate the general rule that the greatest numbers of larvae in the southern North Sea occur in June and July. Larval patches in Text-figs. 1 and 3 have

been numbered and the month of occurrence of the patches are given in Table IV (p. 59); all the southern North Sea concentrations of 1950 and 1951 were found in June and July.

The seasonal occurrence on two parts of the Leith-Skagerrak line is shown in Text-fig. 4, which gives the average number of larvae per sample in each month



TEXT-FIG. 1.—Chart showing the distribution of 10-mile samples with more than 1000 echinoderm larvae during the periods 1932-37, 1938-39 and each year from 1946 to 1949. It should be noted that during the period 1932-37 only the southern part of the North Sea was sampled. The patches found in 1949 have been numbered for the purpose of Table IV, page. 59.

in the section off the Forth (0-170 miles from the Forth) and in the Fisher Bank section (170-350 miles from the Forth). The values for 1948 are given in preference to 1949 since this line was not sampled in April and May, 1949.

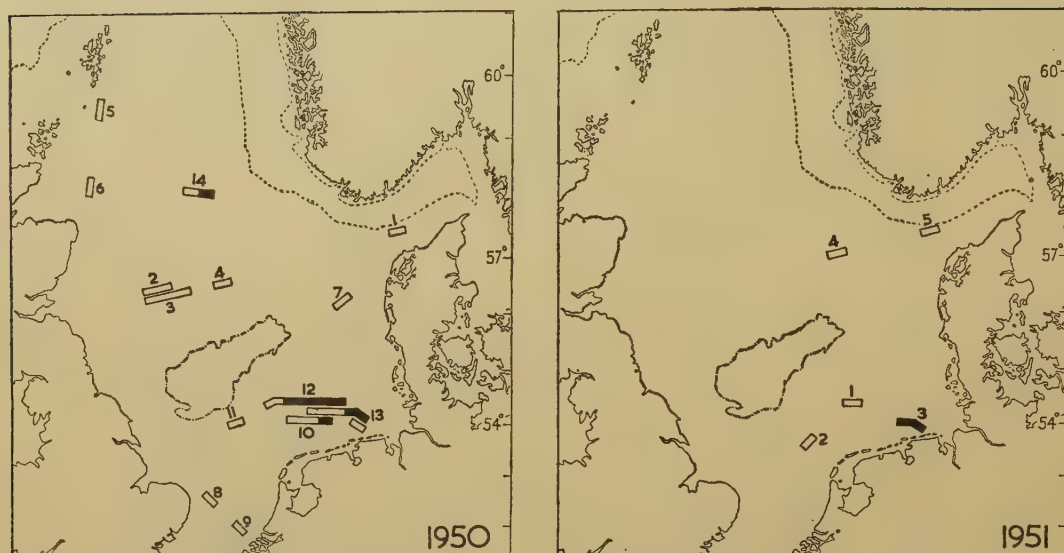
The greatest numbers off the Forth were obtained in April and May in 1948 and 1950, and there was a secondary maximum in August. In 1951 the numbers from March to October were more or less steady. In the Fisher Bank section larvae

were most plentiful in April and May in 1948 and 1950. In 1951 the main concentration occurred in September. In contrast, it may be noted that any concentration of *lamellibranch* larvae off the Forth occurs in August-September and over the Fisher Bank in June-July (Rees, 1954).

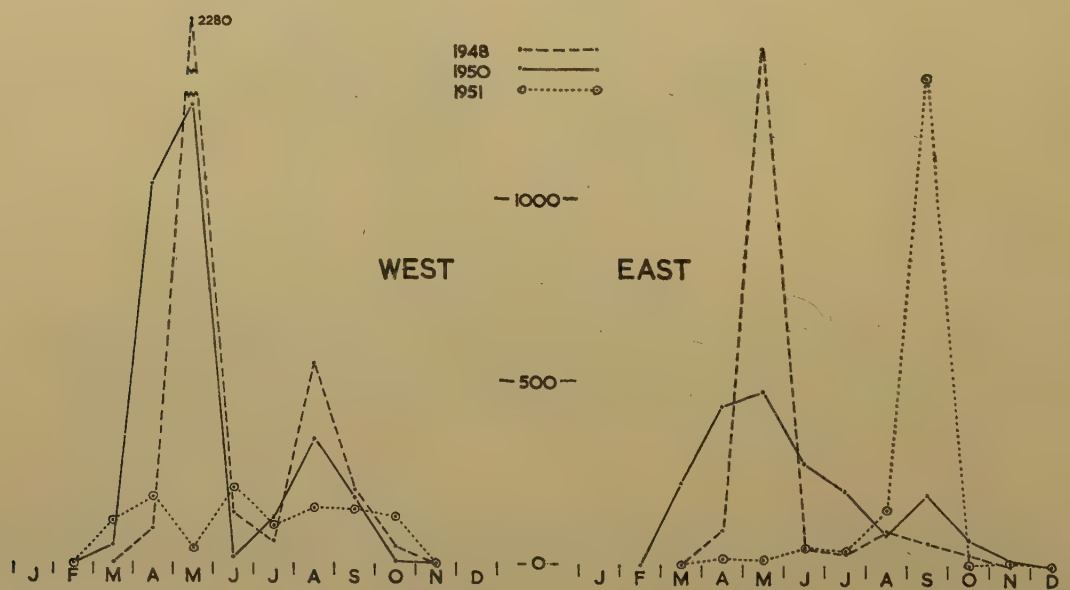


TEXT-FIG. 2.—The black rectangles show the distribution of all 10-mile samples, obtained during the entire Recorder survey, with more than 2000 echinoderm larvae. The density of adults on the bottom, as found in earlier surveys by other workers, is represented by dots, each dot standing for 5 adults (nearest) per m^2 per international square (see p. 57). The hatched boundary line encloses squares not sampled during the quantitative surveys of the bottom fauna.

Of the eight years, 1938–39, 1946–51, during which the Leith–Skagerrak route has been sampled, there was no effective sampling during April–May in three years, 1938, 1947 and 1949. Of the remaining five years, an April–May concentration of echinoderm larvae was found off the Forth in 1946, 1948 and 1950 and no concentration in 1939 and 1951. A heavy concentration over the Great Fisher



TEXT-FIG. 3.—Charts showing the distribution, in 1950 and 1951, of 10-mile samples with 1000–2000 (white rectangles) and more than 2000 (black rectangles) echinoderm larvae. Patches have been numbered for the purpose of Table IV, page 59.



TEXT-FIG. 4.—Graphs showing the average number of echinoderm larvae per 10-mile sample in each month for three years in two sections of the Leith-Skagerrak route. "West" refers to the section off the Forth, "east" to the section over the Great Fisher Bank.

Bank in the autumn has been found only in 1951 of the seven years of adequate sampling, 1938, 1946-51.

THE IDENTIFICATION OF LARVAE.

The larvae of the following species have been found :

<i>Ophiothrix fragilis</i> (Abildgaard).	<i>Psammechinus miliaris</i> (Gmelin).
<i>Ophiocomina nigra</i> (Abildgaard).	<i>Echinus acutus</i> Lamarck.
<i>Ophiactis balli</i> (Thompson).	<i>Strongylocentrotus dröbachiensis</i> (O. Fr. Müller).
<i>Ophiopholis aculeata</i> (Linn.).	<i>Echinocyamus pusillus</i> (O. Fr. Müller).
<i>Amphiura</i> Forbes.	<i>Spatangus purpureus</i> O. Fr. Müller.
<i>Ophiura texturata</i> Lamarck.	<i>Echinocardium cordatum</i> (Pennant).
<i>Ophiura albida</i> Forbes.	<i>Echinocardium flavescens</i> (O. Fr. Müller).
<i>Ophiura robusta</i> Ayres.	
<i>Ophiopluteus dubius</i> Mortensen.	

On the whole, these larvae have been adequately described; the literature concerning nearly all the species has been listed by Thorson (1946). The main fault with the literature lies in the fact that usually only a single stage of a species has been described, generally the latest. For many species, those in which the larva changes considerably during growth, several stages ought to be described before the description is regarded as complete. As an example, the diagnostic character for the larva of *Ophiopholis aculeata* was given as the presence of two median rods (Mortensen, 1927). The majority of larvae of this species observed in Recorder material possessed no median rods, these being present only in the older larvae. However, this particular species has been fully described more recently by Olsen (1943).

Whilst the larva of *Amphiura filiformis* (O. Fr. Müller) has been described (Mortensen, 1931), the larva of *A. chiajei* Forbes is still unknown. The experience of Thorson (1946, p. 350) seemed to show that the larvae of the two species closely resemble each other. The *Amphiura* larvae taken by the Recorder from many parts of the North Sea, and from various times of the year, have also been looked at closely, but no way of separating the larvae of the two species has been found.

Chadwick (1914) referred to the presence of central channels in the skeletal rods of some larvae of *Ophiura albida*. It is possible that these result from poor preservation and may indicate that the material in the core of the processes differs from that on the outside.

Thorson (1946) gives good reason for accepting *Ophiopluteus compressus* as the larva of *Ophiura robusta*.

The larva tentatively assigned to *Ophiura affinis* Lütken has a very simple form (Mortensen, 1927). It is probable that if such larvae have been taken by the Recorder they were unrecognized or unrecognizable as echinoderm larvae. *O.*

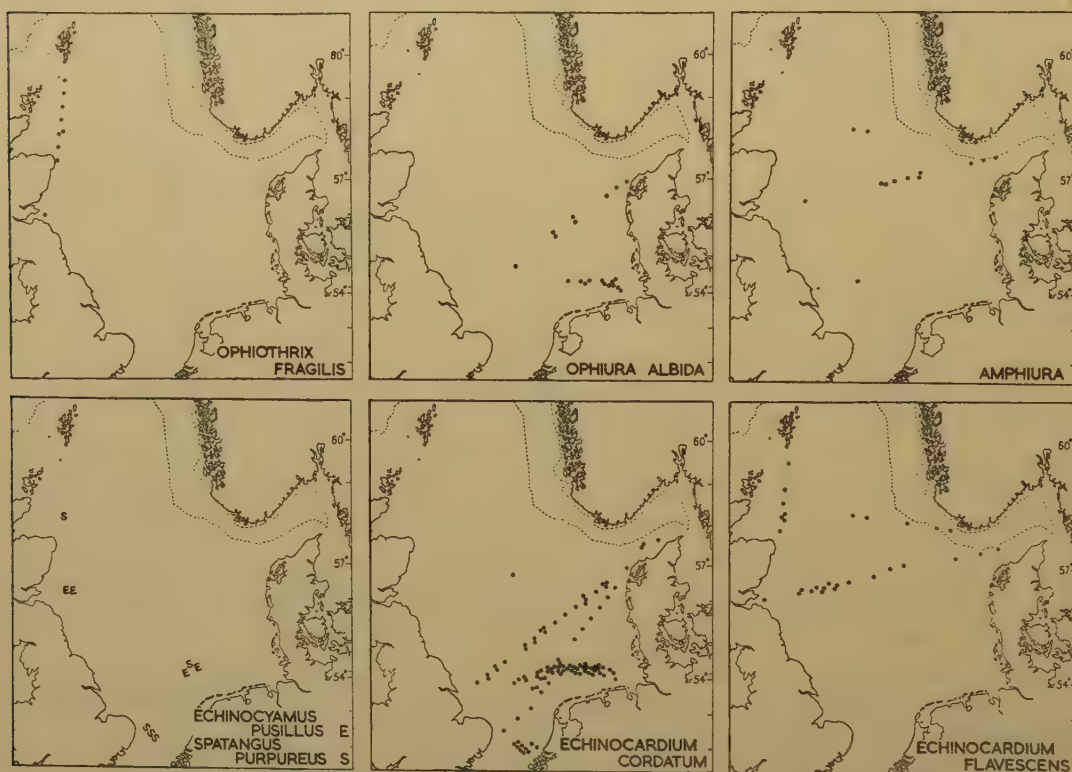
affinis larvae would be expected to be fairly common, but nevertheless no echinoderm larvae have yet been seen in the Recorder material which cannot be assigned to some other species. This could be taken as very indirect evidence that *O. affinis* larvae do not have a well-developed ophiopluteus form.

The characters used for the identification of the larvae of *Spatangus purpureus*, *Echinocardium cordatum* and *E. flavescens* have recently been described (Rees, 1953).

DISTRIBUTION OF THE SPECIES.

The approximate quantitative distributions of the larvae of various species are shown in Plates XI and XII. In most cases the month of occurrence is indicated by the use of circular, square or triangular symbols.

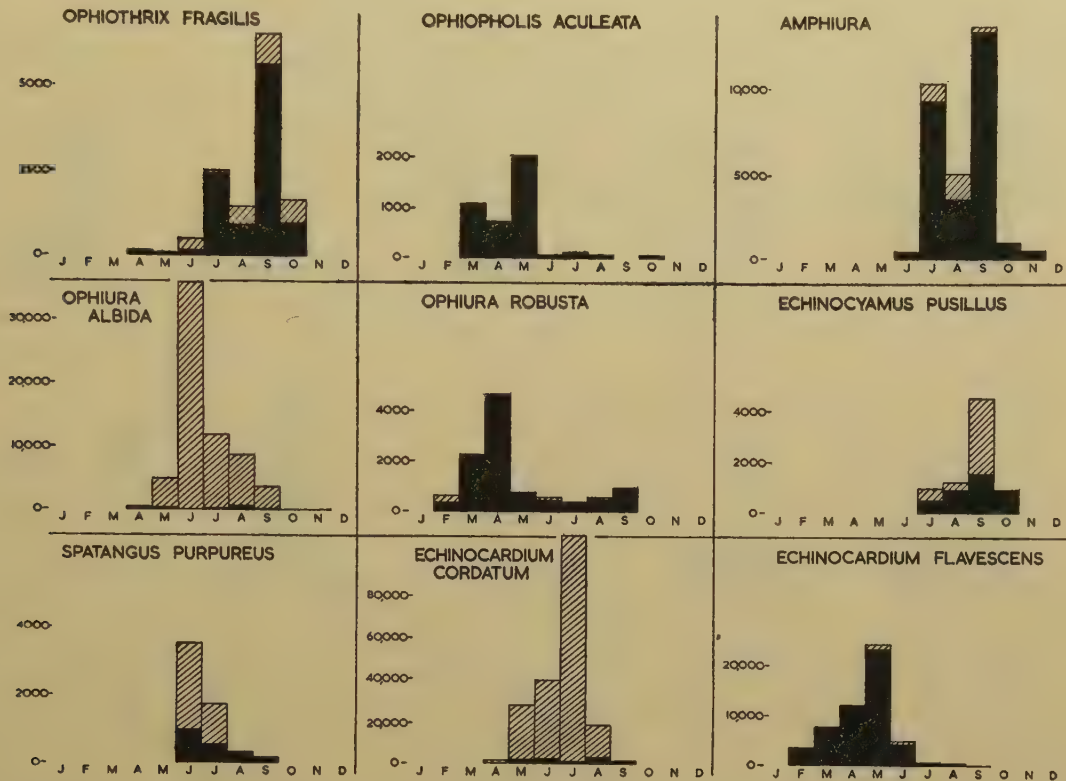
It was explained above that only samples containing more than 480 larvae in the 1949 and 1950 material, and more than 160 larvae in the 1951 material, were re-examined for species. The reduction in the lower limit in the 1951 material introduces a difference into the charts of distribution. If every sample had been re-examined, as in the case of the lamellibranchs, the number of small white and



TEXT-FIG. 5.—Charts showing the distribution of all samples taken in 1949, 1950 and 1951 which contained more than 500 specimens of various species.

small black symbols (see Scale Key in Plate XI) would have greatly increased in the 1949 and 1950 charts, but there would have been no increase in the large white and higher symbols. In the 1951 charts the number of small white symbols would have increased, but the small black and higher symbols would not have increased.

Text-fig. 5 gives a simple overall picture of the distribution of various species. Dots show the positions of all samples which contained more than 500 larvae of the species illustrated.

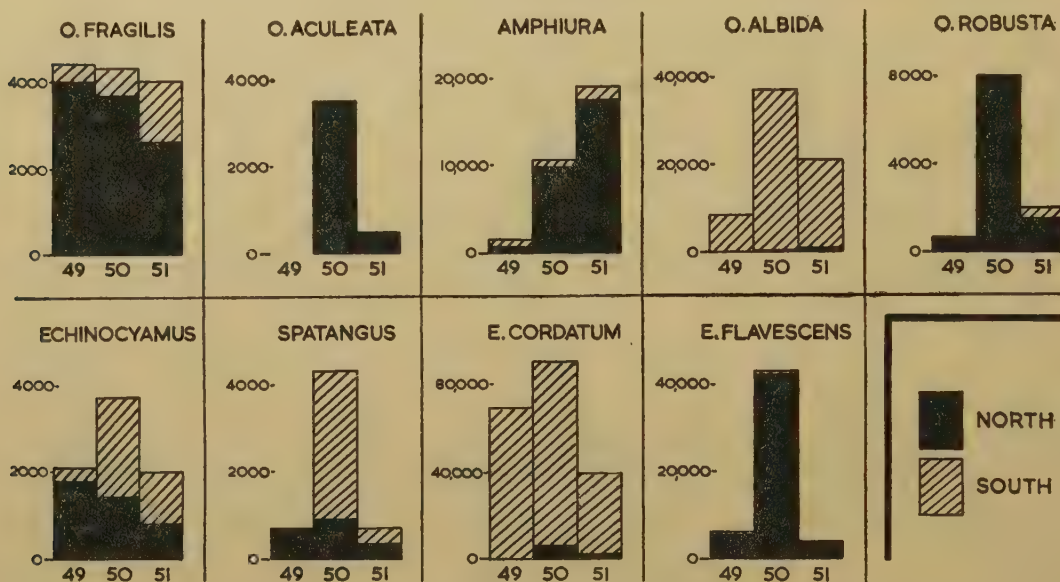


TEXT-FIG. 6.—Histograms giving the total number of larvae of various species obtained in each month, 1949 to 1951 combined, over the entire North Sea. The numbers obtained north and south of the line Newcastle to the Skaw are distinguished by the solid and hatched portions respectively.

The histograms in Text-fig. 6 show the estimated number of larvae of various species obtained in each month, 1949 to 1951 combined. The black portion shows the number north of the line Newcastle to the Skaw, and the hatched portion the number south of this line.

Text-fig. 7 shows the estimated total number of larvae of the species, included in Text-fig. 6, which have been obtained in each year, north and south of the Newcastle-Skaw line. The values for 1949 are affected, in comparison with those for

1950 and 1951, by some differences in the taking of records. There were no Leith-Skagerrak records in April and May, 1949, so that the numbers of the northern forms which thrive in the spring (*Echinocardium flavescens*, *Ophiura robusta*, *Ophiopholis aculeata*) are probably too low in comparison. Furthermore, the London-Copenhagen (G) line did not sample into the Heligoland Bight in 1949, whereas it did so in 1950 and 1951. In consequence, the larvae which occur in immense numbers in the Bight (*E. cordatum*, *Ophiura albida*) are probably too low in number in 1949 compared with the two following years.



TEXT-FIG. 7.—Histograms giving the total number of larvae of various species obtained in each year over the entire North Sea. The numbers obtained north and south of the line Newcastle to the Skaw are distinguished by the solid and hatched portions respectively.

Comment on the species will be restricted to features not immediately apparent from the distributions illustrated:

Ophiocomina nigra.—Only a single specimen was seen, 30 miles off the Forth in October, 1951.

Ophiactis balli.—Larvae were found from July to September, with most observations in September.

Amphiura.—Very few larvae were obtained after September (Text-fig. 6). Mortensen (1920) found, at Kristineberg, that *A. chiajei* began to breed about the middle of September. If the breeding time in the North Sea agrees with this, it would appear that the very great majority of *Amphiura* larvae obtained were those of *A. filiformis*.

This is the only larva which was more common in 1951 than in the two previous years (Text-fig. 7). It was responsible for the considerable population of total

larvae on the Leith-Skagerrak line in September. This was an unusual occurrence for no comparable concentration occurred at this time during the earlier years, 1938, 1946-1950.

Ophiura texturata.—Larvae were observed in thirteen samples only, from May to September, with no clear indication of the season of maximal abundance.

Ophiura albida.—There is considerable resemblance between the distribution of these larvae and those of *E. cordatum* (Text-fig. 5), but *O. albida* larvae occur in greatest number rather earlier, in June.

Ophiura robusta.—The larvae of this species have been found in the southern North Sea (Plate XI) although it is said that *O. robusta* is distributed on the east British coast only from the Shetlands to Durham (Mortensen, 1927).

Ophiopluteus dubius.—Larvae were observed in two samples over the Norwegian Channel, south-west of Norway, in March, 1950.

Psammechinus miliaris.—Larvae were obtained from June to October, but were always scarce.

Echinus acutus.—Larvae were observed only in March and April.

Strongylocentrotus dröbachiensis.—Larvae were recorded only in March and May.

DISCUSSION.

Marshall (1948, Text-Fig. 7) charted the population densities of bottom-living echinoderms as determined in the surveys of Davis (1923, 1925) and Stephen (1934). This chart may be further filled by also using Petersen's (1914) results for the region off the Danish coast in the same way as was done for bottom-living lamellibranchs (cf. Rees, 1951, p. 111): 0 in L13, 140 in L11, 7 in M14, 36 in M13, 140 in M12, 110 in M11, 5 in N15, 67 in N13, 25 in N12, 95 in O13.

It was noted that the major concentrations of lamellibranch larvae were poorly correlated with the distribution of adults as found in the bottom surveys (Rees, 1951, p. 120). In Text-fig. 2, dots have been inserted to indicate the adult echinoderm population as given in Text-fig. 7 of Marshall (1948), each dot representing five individuals per square metre per international square. Here again a poor association between adults and larvae is shown. In particular, the adult population density in the Heligoland Bight did not reflect the intense larval concentrations which have been found here.

There is a marked difference between the composition of the larval populations in the northern half and in the southern half of the North Sea, Newcastle to the Skaw being taken as the arbitrary boundary. This difference is brought out in Table II which gives the estimated total number (to the nearest 100) of larvae of the dominant species obtained during 1949 to 1951, and the percentage that each is of the total. The species are arranged in order of abundance over the entire North Sea.

In the north *Echinocardium flavescens* and *Amphiura* were the dominant larvae. Over a longer period of years it is likely that the percentage of *Amphiura*

TABLE II.—Giving the number of Hundreds of Larvae, and the Percentages, of the Dominant Species obtained during 1949 to 1951.

	North Sea.		Northern North Sea.		Southern North Sea.	
	Hundreds.	%.	Hundreds.	%.	Hundreds.	%.
<i>Echinocardium cordatum</i>	198	51	8	7	190	71
<i>Ophiura albida</i>	65	17	1	+	64	24
<i>Echinocardium flavescens</i>	52	13	51	43	1	+
<i>Amphiura</i>	31	8	28	24	3	1
<i>Ophiothrix fragilis</i>	13	3	10	9	3	+
<i>Ophiura robusta</i>	10	3	10	9	+	+
<i>Echinocyamus pusillus</i>	8	2	4	3	4	1
<i>Spatangus purpureus</i>	6	1	2	1	4	1
<i>Ophiopholis aculeata</i>	4	1	4	3	0	0

would be lower; the abundance of total echinoderm larvae, of which the great majority were *Amphiura*, on the Leith-Skagerrak line in September, 1951, was an unusual feature in comparison with the seven earlier years. It is also possible that many more *E. flavescens* larvae would have been obtained if the Leith-Skagerrak records of April and May, 1949, had been taken. In the south *Echinocardium cordatum* predominated by far, and *Ophiura albida* was the only other species which occurred in abundance.

A rough idea of the composition of the echinoderm bottom fauna of the southern North Sea can be obtained by summing the number of specimens of each species obtained by Davis (1925, Appendix 1) and expressing it as the percentage of the total echinoderms obtained. Similarly, the results of Stephen (1934, Table II) can be used for the northern North Sea. Table III compares the percentages of species of adults in bottom fauna surveys and of larvae obtained in the Recorder survey during 1949 to 1951.

TABLE III.—Comparing the Percentage Composition of the Bottom Fauna and that of the Larvae obtained during 1949 to 1951.

	Northern North Sea.		Southern North Sea.	
	Adults.	Larvae.	Adults.	Larvae.
<i>Echinocardium cordatum</i>	2	.7	63	71
<i>E. flavescens</i>	24	43	4	+
<i>Echinocyamus pusillus</i>	9	3	2	1
<i>Ophiura albida</i>	+	+	4	24
<i>Ophiura affinis</i>	28	0	+	0
<i>Amphiura</i>	28	24	25	1
<i>Echinus acutus</i>	7	+	0	0

In the north, the percentage of *Ophiura affinis* differed greatly between adults and larvae. The possibility was raised above (p. 53) that the presumed larva of this species is so simple that it is unrecognized or unrecognizable in the damaged

Recorder material. During the grab surveys only material from soft bottoms was taken and species confined to hard bottoms were not obtained; this fact probably explains the fairly high percentages of larvae of *Ophiothrix fragilis* and *Ophiura robusta* in the north (Table II), without any corresponding adults in the grab survey. In the south, there was an interchange of the percentage values between *Ophiura albida* and *Amphiura*.

The main concentrations found in 1949 to 1951 have been numbered in Text-figs. 1 and 3. The percentage composition of the larval population in each numbered patch is given in Table IV, together with the month in which it was found.

TABLE IV.—*Giving the Percentage Composition of Patches in 1949 to 1951.*

The patches are shown and numbered in Text-figs. 1 and 3.

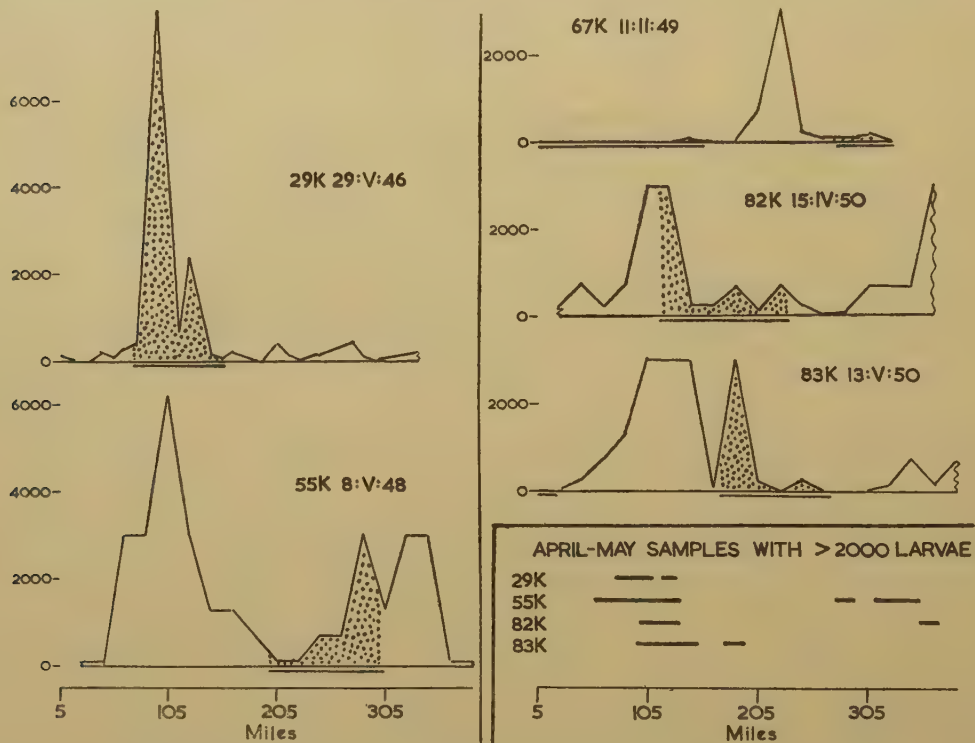
Patch.	Month.	<i>E. cordatum.</i>	<i>E. flavescens.</i>	<i>Spatangus.</i>	<i>O. albida.</i>	<i>O. robusta.</i>	<i>Amphiura.</i>
1949.							
1	II	—	93	—	—	7	—
2	V	76	10	—	14	—	—
3	V	76	7	—	17	—	—
4	V	99	—	—	—	—	—
5	VI	100	—	—	—	—	—
6*	VII	83	—	—	—	3	—
7	VII	100	—	—	—	—	—
8	VII	100	—	—	—	—	—
9	VII	98	—	—	2	—	—
1950.							
1*	IV	—	70	—	—	17	—
2	IV	—	96	—	—	4	—
3	V	—	100	—	—	—	—
4	V	—	96	—	—	4	—
5*	V	3	65	—	—	6	—
6	V	5	95	—	—	—	—
7	V	93	7	—	—	—	—
8	VI	73	—	22	5	+	—
9	VI	93	—	—	—	—	—
10	VI	27	—	—	73	—	—
11	VII	84	—	7	7	—	—
12	VII	99	—	1	—	—	+
13	VII	98	—	+	2	—	+
14	VII	—	—	2	—	2	94
1951.							
1	VI	53	—	—	47	—	—
2	VI	95	—	—	5	—	—
3	VII	50	—	—	50	—	—
4	IX	—	—	—	—	—	100
5	IX	—	—	—	—	—	100

* Also in 1949, 6, *Echinocyamus* 14%; 1950, 1, *O. aculeata* 10%; 5, *O. aculeata* 20%.

The table shows clearly the predominance in the northern half of the North Sea, of *E. flavescens* in the spring (Feb., April-May) and of *Amphiura* later in the

year (July, September). In the south *E. cordatum* was, of course, predominant, but *O. albida* was more abundant in one or two of the early patches in the Heligoland Bight.

It can be said that *E. flavescens* is by far the dominant species in any major concentration of larvae in the northern half of the North Sea before the end of May. It is, in fact, permissible to regard the numbers of total echinoderm larvae as virtually the numbers of *E. flavescens* during the first five months of the year.



TEXT-FIG. 8.—Graphs giving the number of echinoderm larvae in each 10-mile sample of all Leith-Skagerrak records, taken from January to May, which had in any sample over 2000 larvae. Sections of records taken at night are marked by a double base line and portions of graphs relating to larvae taken at night dotted.¹ At the bottom right, lines mark the position of all April-May samples with over 2000 larvae.

Text-fig. 8 shows the distribution of larvae along all Leith-Skagerrak records, taken before the end of May, which contained more than 2000 larvae in any sample. Of the years under review, April-May records were obtained only in 1946, 1948, 1950 and 1951, and a major concentration was found in May in all except 1951. Inset in Text-fig. 8 are shown the positions where samples containing over 2000

¹ The distinction between samples taken by night and by day which is made in Text-figs. 8-10 is not considered to be relevant to this report. It is anticipated, however, that this information will be required on a future occasion.

larvae have been found on April-May records. There is clearly a regularity here which may be illustrated by the fact that, in all four records, the sample taken 105 miles from the Forth contained a great number of larvae, in 1946 and 1948 the greatest number. In February, 1949, on the other hand, the concentration was found over the Great Fisher Bank.

Text-fig. 8 shows that these concentrations were not only heavy but also narrow along the west-east axis. A detailed consideration of the distribution of the larvae of *Mytilus edulis* in May, 1950, when extra records were taken, led to the conclusion that similar narrow patches of *Mytilus* larvae on the Leith-Skagerrak records were due to sampling across elongated, narrow distributions. These were called band distributions (Rees, 1954). The data concerning *E. flavescens* have been similarly treated. The distributions of *E. flavescens* on the Aberdeen-Lerwick (A) record, and on the north and south legs of the special records, 7 TB and 12 TA, are shown in Text-fig. 9 (see charts in Text-fig. 9 for courses and dates). The distributions of total echinoderm larvae on the Leith-Skagerrak records from March to September are shown in Text-fig. 10. Various peaks in abundance have been numbered in Text-figs. 9 and 10 and the numbers transferred to two charts in Text-fig. 9.

The patches numbered 1a, 1b and 1c occurred in a closely confined area ; the 12 TA record was not long enough to sample right through concentration 1c. The great majority of the larvae in patch 1a were old, with well-developed postero-lateral arms. Whilst the larvae in patches 1b and 1c were distinctly more developed, it is very unlikely that the population of larvae in patch 1a was still planktonic 28 and 33 days later to be re-sampled as patches 1b and 1c. MacBride (1914) found that the entire development, up to the end of metamorphosis, of the allied species *Echinocardium cordatum*, took only four weeks in culture and it is improbable that the rate of development of *E. flavescens* larvae was so much slower that 1a and 1b were samples of the same population. It seems, then, that there was a recruitment and loss of larvae in the area where patches 1 were found. This change over of the larvae fits in well with the view that patches 1 and 2 were transections of a single band distribution, as in the examples of *Mytilus* larvae (Rees, 1954) and other organisms to be dealt with in a later ' Bulletin.'

The sharp peak of numbers comprising patch 3 (83K) occurred in the same sample which contained a very great number of *Mytilus* larvae. This was the most striking concentration of *Mytilus* larvae obtained during this period and is that numbered 3 in Text-fig. 10 of Rees (1954).

The patches 4 (a or b), 5 and 6 may, perhaps, be sections of a single band distribution. Numbers decreased greatly from north-west to south-east, and it is possible that larvae had become too scarce for this band to be shown further south, on the Leith-Skagerrak route (84K). It is uncertain whether the very small patch 7 (84K) should be regarded as an extension of patches 5 and 6 or the surviving residue of the earlier concentration here (3).

The distributions of larvae of *E. flavescens* and *Mytilus edulis* only partially

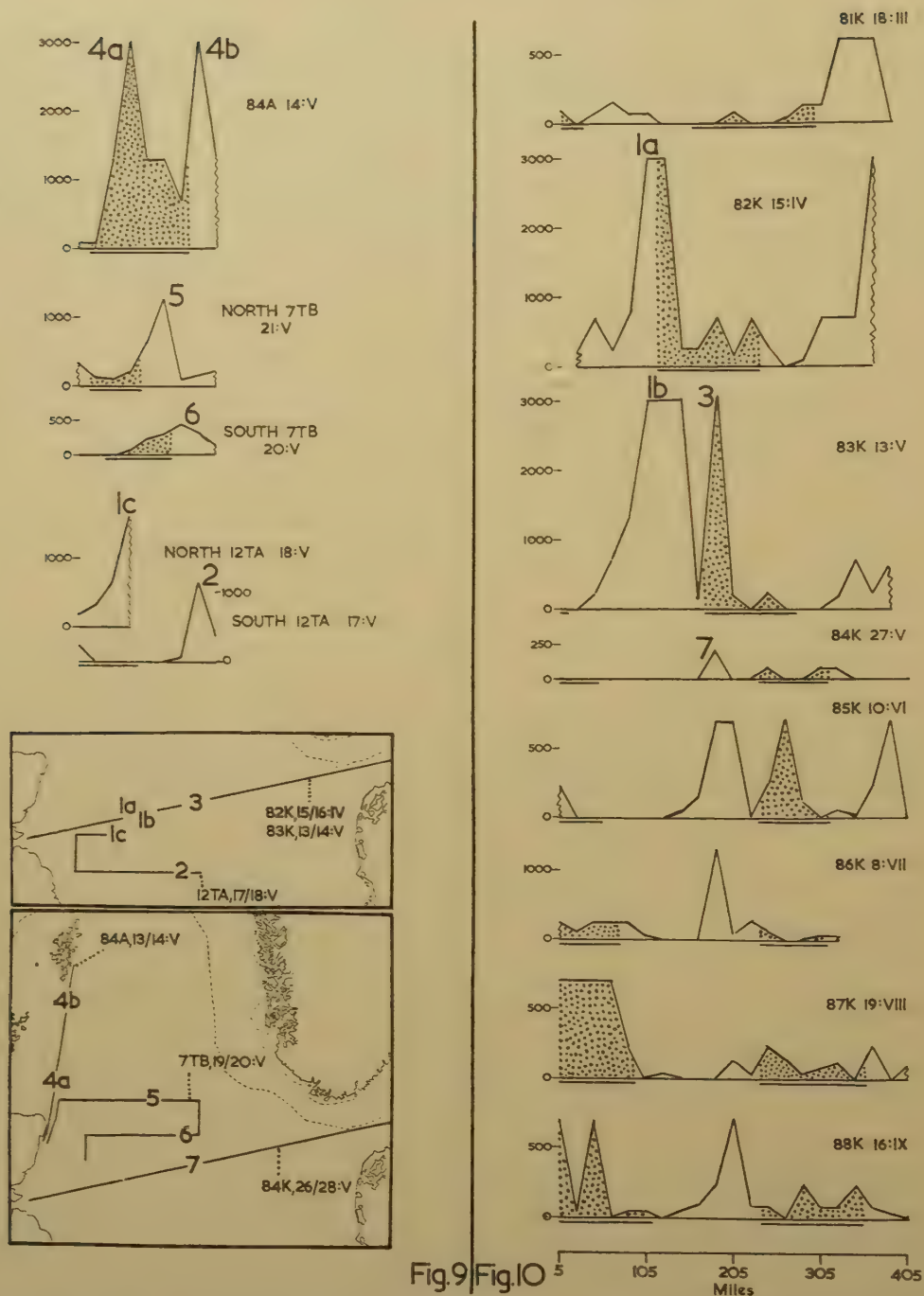


Fig.9 Fig.10

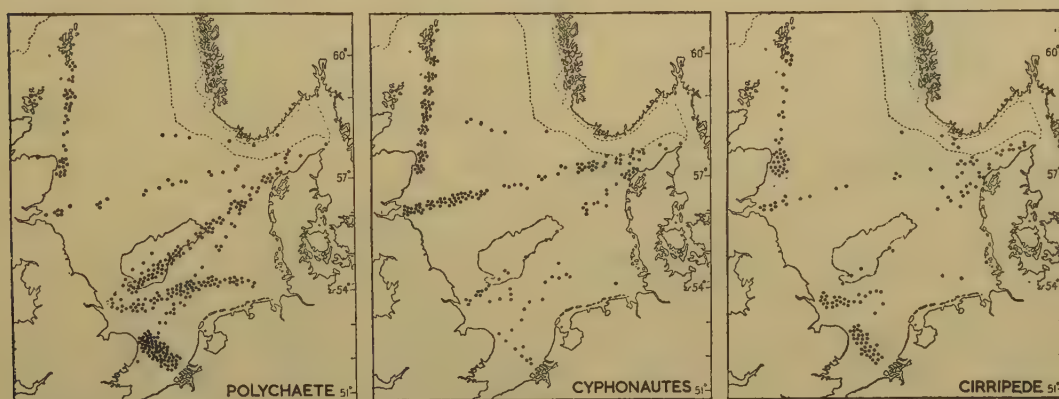
TEXT-FIGS. 9 and 10.—The charts in Text-fig. 9 show the routes and dates of records taken in May, 1950, the graphs show the number of echinoderm larvae in each 10-mile sample along some of these records. The graphs in Text-fig. 10 show the number of larvae in each sample of the Leith-Skagerrak records from March to September, 1950. Appropriate peaks in the graphs in Text-figs. 9 and 10 have been numbered and the location of these peaks shown on the charts in Text-fig. 9. In all graphs the sections taken at night are shown by a double base line and the dotted portions of the graphs. See footnote p. 60.

coincided over this period ; the only concentrations of *E. flavescens* which coincided with concentrations of *Mytilus* larvae are those numbered 3 and 6 in Text-figs. 9 and 10. In this connection, two points may be noted. The first is that the seasonal occurrence of *E. flavescens* larvae was earlier than of *Mytilus* larvae. On the earliest of the records, 82K, April 15th, *E. flavescens* larvae were abundant whilst *Mytilus* larvae were as yet rare, and very few *E. flavescens* larvae were found at the end of May when *Mytilus* larvae were still abundant (cf. Text-fig. 10 with Text-fig. 10 of Rees, 1954). The second is that the *E. flavescens* and *Mytilus* larvae concerned may have originated from different places. *Mytilus edulis* is essentially a coastal form whereas *E. flavescens* normally lives in deeper water.

A tentative representation of the distribution of *Mytilus* larvae in the spring of 1950 gave successive bands as occurring further towards the east (Rees, 1954, p. 41). Text-fig. 10 shows that there was a similar apparent movement of echinoderm patches on the Leith-Skagerrak line from April to June. A comparison between the graphs for 83K and 85K illustrates this feature very well. As in the case of *Mytilus*, a switch of the main concentration from the centre of the route in July to the Forth side in August was also shown. It may be noted that *E. flavescens* was not a dominant species in the concentrations from June onwards.

DISTRIBUTION OF OTHER LARVAE.

Polychaete, cyphonautes, cirripede and actinotrocha larvae have rarely been found in appreciable numbers in Recorder samples. Almost the whole of the



TEXT-FIG. 11.—Charts showing the distribution of all samples taken during 1947 to 1951 in which polychaete, cyphonautes and cirripede larvae were found to be present.

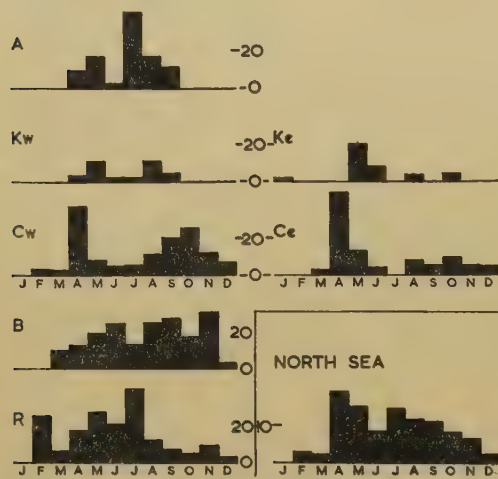
post-war information available consists of records of only the presence, with no statement of numbers, of these larvae in the samples.

Text-fig. 11 illustrates the distribution of all samples taken in 1947 to 1951 in which the larvae of the first three groups have been recorded. Some minor adjust-

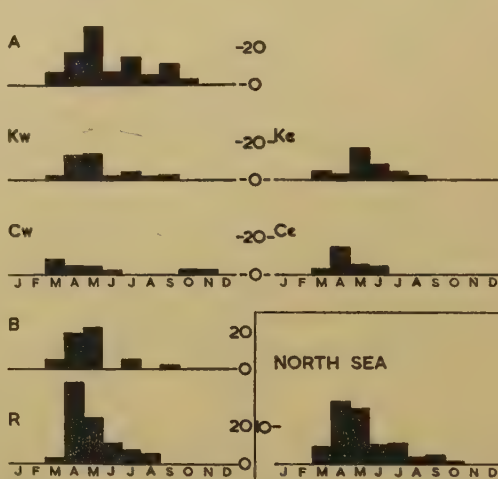
ments have been made to avoid bias due to the taking of more than one record along a route in a month.

The histograms in Text-fig. 12 show the percentage of the samples which contained these larvae in each month, 1947 to 1951 combined, along the main Recorder routes, the Leith-Skagerrak and Hull-Copenhagen lines being divided into western and eastern halves. The percentage for the entire North Sea is also

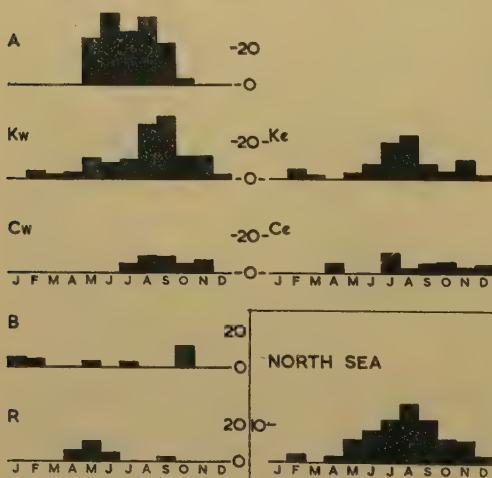
POLYCHAETE



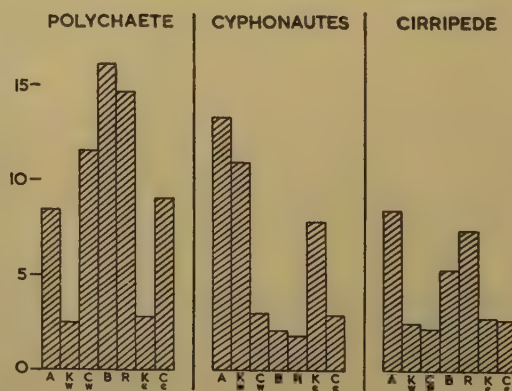
CIRRIPEDA



CYPHONAUTES



PERCENTAGE OCCURRENCE



TEXT-FIG. 12.—Histograms giving the percentage of samples in each month, 1947 to 1951 combined, in which polychaete, cyphonautes and cirripede larvae were found along the Aberdeen-Lerwick (A) route, the western (Kw) and eastern (Ke) parts of the Leith-Skagerrak route, the western (Cw) and eastern (Ce) parts of the Hull-Copenhagen route the Hull-Bremen (B) route and Hull-Rotterdam (R) route. At the bottom right, the number of samples which contained these larvae along the various routes are expressed as a percentage of the total number of samples taken.

given. Also in Text-fig. 12 (bottom right) are histograms giving the overall percentage of samples containing larvae along each route.

Polychaete larvae.—These larvae were most frequently found in the southern half of the North Sea and rarely in the central North Sea (Text-figs. 11 and 12). Larvae were found most frequently in April along the southern edge of the Dogger Bank (C west) and towards the Danish coast (C east). There is an indication of a north to south succession in high frequency starting in July in the north-west (A), in August off the Forth (K west), in October off the Humber (C west) and in November in the southern North Sea (B).

One major patch of larvae has been recorded, off the Aberdeenshire coast in July, 1946, when two adjacent samples contained more than 2000 larvae.

Cyphonautes larvae.—Marshall (1948) has given the distribution of these larvae during 1938 and 1939. He pointed out that the north-west was by far the most important productive area, the entrance to the Skagerrak being the only other region where larvae were found in any quantity. This is generally confirmed by the distributions of 1947 to 1951 except that records were relatively frequent off the Forth (Text-figs. 11 and 12). Records off the Forth occurred most frequently in August and September which, related to the monthly frequency in the north-west, suggests that larvae may have been transported southwards in the early stage of the autumn influx. Of the years 1947 to 1951, larvae occurred least frequently off the Forth in August and September in 1947, a year in which the autumn influx was much delayed (Tait, 1949). The greatest frequency in these months was in 1951, at a time when a major concentration of lamellibranch larvae was sampled off the Forth, a concentration which appeared to be related to the autumn influx (Rees, 1954).

Cirripede larvae.—Cirripede larvae were mainly restricted to coastal areas and, in all regions, the greatest frequency occurred early, around April-May (Text-figs. 11 and 12).

The early maxima of larvae in the North Sea correspond with findings in other areas. At Millport the greatest number of cirripede nauplii were obtained in March in each of four years (Pyefinch, 1948, Table VIII) and at Port Erin in March and April over many years (Johnstone, Scott and Chadwick, 1924).

Actinotrocha larvae.—The larvae of Phoronis were found rarely, altogether in less than 40 samples throughout 1946 to 1951. A distinct patch occurred in July, 1946, off the Aberdeenshire coast, more than 1000 larvae being obtained in the same samples, mentioned above, which contained the large numbers of polychaete larvae. Elsewhere, larvae were obtained off the Forth and along the southern edge of the Dogger Bank, mostly in August.

SUMMARY.

1. The main concentrations of echinoderm larvae occurred in the eastern part of the southern North Sea, particularly within the Heligoland Bight.

2. The distribution of larvae as a whole was poorly correlated with that of the adults as found in earlier bottom surveys.

3. The greatest numbers of larvae in the southern North Sea occurred in June-July. Along the Leith-Skagerrak route the greatest numbers occurred, as a rule, in April-May, with secondary maxima in August-September.

4. The approximate quantitative distributions of larvae of various species during 1949-51 are presented in charts (Plates XI and XII), the seasonal occurrence in Text-fig. 6 and the comparative numbers from year to year in Text-fig. 7.

5. Larvae of *Echinocardium flavescens* and *Amphiura* were dominant in the northern half of the North Sea, and larvae of *Echinocardium cordatum* and *Ophiura albida* in the southern half.

6. There was a fairly good agreement between the specific composition of the larval populations and the adult populations taken in the early bottom surveys, except that *Ophiura albida* was the second most abundant echinoderm in the larval population of the south, whereas *Amphiura* occupied this place in the bottom fauna.

7. *Echinocardium flavescens* was by far the dominant species in any major concentration of larvae in the northern North Sea in the first five months of the year. The profiles of concentrations found in April-May along the Leith-Skagerrak route show marked uniformity.

8. The distributions of *E. flavescens* larvae in May, 1950, have been presented. The distributions may be interpreted as being narrow and elongated, or band distributions, as in the case of larvae of *Mytilus edulis* (Rees, 1954). *E. flavescens* larvae appeared in large numbers distinctly earlier than *Mytilus* larvae.

9. There was an apparent west to east movement of concentrations of echinoderm larvae along the Leith-Skagerrak route from March to June.

10. The larvae of Polychaeta, Cirripedia, Bryozoa and Phoronidea have rarely been found in appreciable numbers in Recorder samples. The distributions of these larvae are presented only very briefly.

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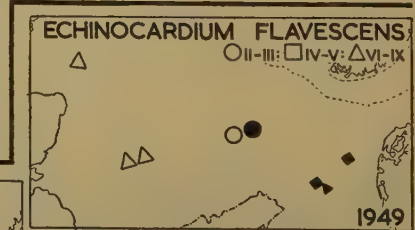
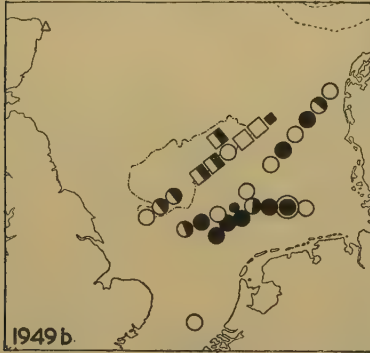
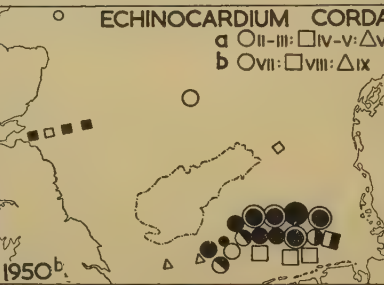
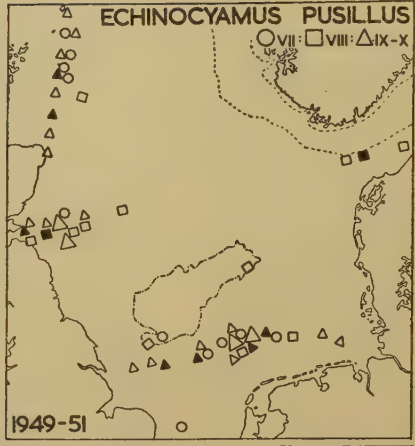
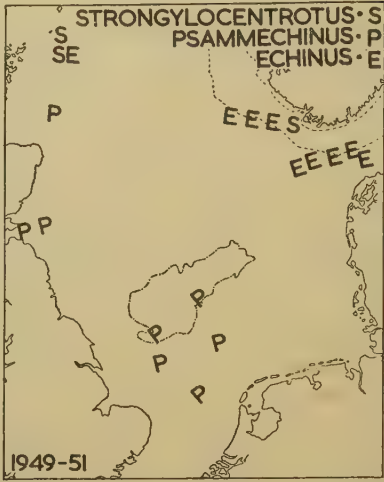
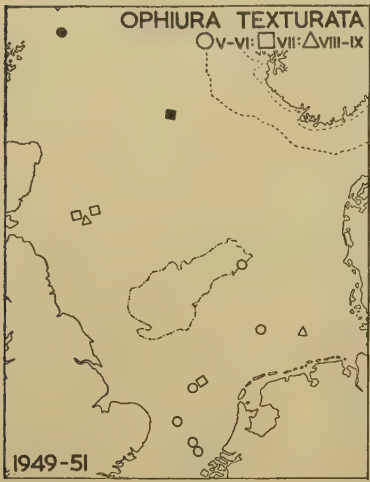
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EXPLANATION OF PLATES XI AND XII.

Charts showing the distributions of species of echinoderm larvae in 1949 to 1951. In some cases the distributions in all three years are combined into single charts, in others the years are charted separately. The months of occurrence are indicated by the use of circular, square and triangular symbols, as shown near each specific name. The scale of symbols used to give broad indications of numbers is given on Plate XI.





CONTINUOUS PLANKTON RECORDS: THE DECAPOD LARVAE IN THE NORTH SEA, 1950-51

BY

C. B. REES, D.Sc.

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INTRODUCTION

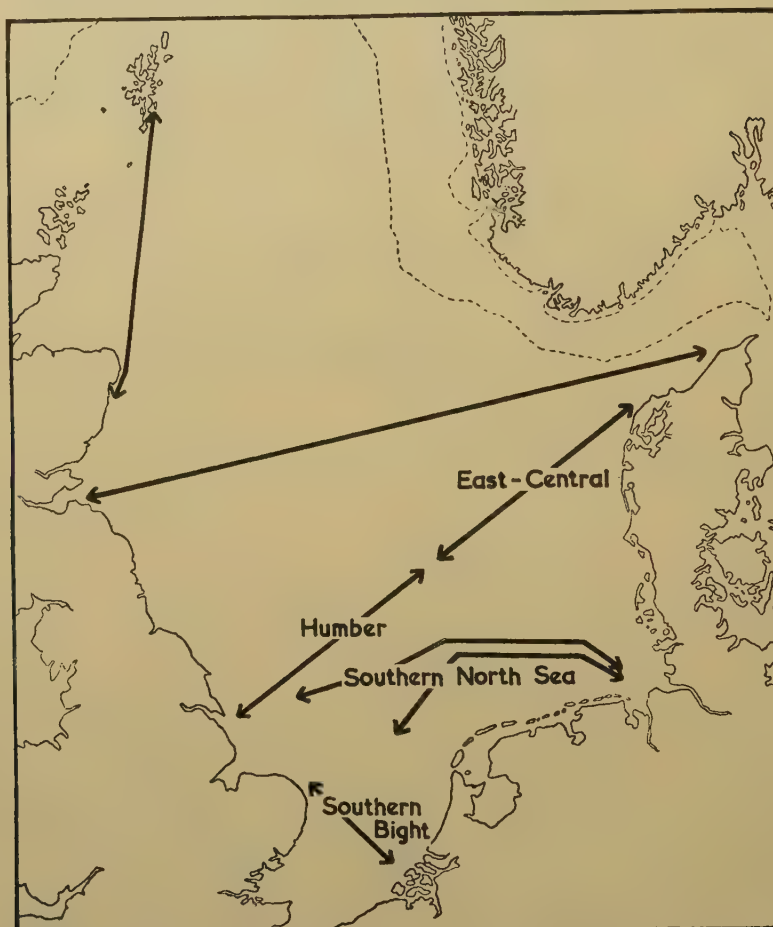
A comprehensive study of the distribution of the planktonic larvae of bottom-living animals in the North Sea was commenced in 1946, as part of the Continuous Plankton Recorder Survey. Reports have so far been presented on the distribution of decapod crustacea larvae up to 1949 (Rees, 1952), of lamellibranch (Rees, 1951, 1954*a*), echinoderm and some other larvae (Rees, 1954*b*) up to 1951. In order to bring the decapod larvae into line with the other two main groups, it is necessary to cover the years 1950 and 1951 and it is the purpose of this brief report to do this.

Rae (1952) has described the routine method of analysis of the plankton. The standard Recorder routes used during 1950 and 1951 are shown in Text-fig. 1. The regions named there are the same as those used in the 1947 to 1949 report but the regions "north-west", "Forth," and "Skagerrak" have not been retained (Rees, 1952, Text-fig. 1). An important point to note is that the London-Copenhagen route which previously ran via Skaw has, since 1950, run via the Kiel Canal.

The work on the decapod larvae during 1947 to 1949 was intended to establish the general pattern of distribution and as many larvae as possible were examined. All the larvae in every 10-mile sample¹ were examined in the 1947 and 1948 records,

¹ Each record is cut up into lengths of silk corresponding to 10 miles of tow of the Recorder. The plankton retained by each length of silk is conveniently referred to as a 10-mile sample.

and all the larvae in alternate samples in the 1949 records. After these three years it was felt that the number of larvae identified could be substantially reduced and that, the general pattern of distribution having been established, the aim should be merely to recognize and assess any trends and unusual occurrences. Consequently,



TEXT-FIG. 1.—Chart showing the usual Recorder routes in the North Sea during 1950 and 1951, together with the regional terms used in this report.

only those samples in which 12 or more decapod larvae had been found during routine analysis were re-examined for species. In addition, it was later found desirable to identify all the larvae in alternate samples of the "Humber" and "Southern North Sea" regions (Text-fig. 1) from July to September in each year.

It is important to realize the implication of this considerable restriction of the number of samples re-examined for species when comparing the results with those of previous years. A reasonably good idea of the quantitative distribution of the

common species was obtained for 1950 and 1951, but the opportunities for finding the uncommon species were greatly reduced. For example, no larvae taken from October, 1950, to June, 1951, were specifically identified. Therefore, whilst the numbers, or average numbers, of the common species obtained in 1950 and 1951 may reasonably be compared with the numbers in the earlier years, the numbers of the uncommon species are merely minimal values as compared with the more exact values for the years 1947 to 1949.

Since the specific recording of the uncommon species thus depended so much on the incidence of the common species, it is not appropriate to deal with all the observations at this stage. Only the distributions of the common species, such as *Upogebia deltaura* and *Callianassa subterranea*, and those of particular interest are considered.

DISTRIBUTION OF TOTAL DECAPOD LARVAE.

The great bulk of larvae were obtained in the period July to September. The number of larvae in each sample during these three months of the years 1949 to 1951 is shown in Text-fig. 2. The distributions from January to June are shown in a single chart for each year, the observations being numbered according to the month in which they were taken. The category of 0-11 animals per 10-mile sample is not given in these combined charts so that the full extent of sampling from January to June is not shown; it is given, however, by Rae (1952, 1953).

The graphs in Text-fig. 3 show the average number of larvae per 10-mile sample per record or part of record in the regions in the southern half of the North Sea (Text-fig. 1).

From the two text-figures it appears that decapod larvae were most numerous in the "Humber" region in 1949. This stands out most clearly in the period April to June in Text-fig. 2. The absence of Hull-Copenhagen records between June 1st and August 18th, 1950, and between August 18 and November 3, 1951, leaves some doubt about the latter halves of the two years. The available records, however, strongly suggest that numbers of larvae along the whole Hull-Copenhagen route were reduced in 1950 and 1951 as compared with 1949.

Another prominent feature was the dense concentrations of larvae in the southern North Sea in 1951. No such heavy concentration was found in 1950 though sampling was adequate. The Hull-Bremen record of August, 1949 was, unfortunately, too short for a fair comparison to be made.

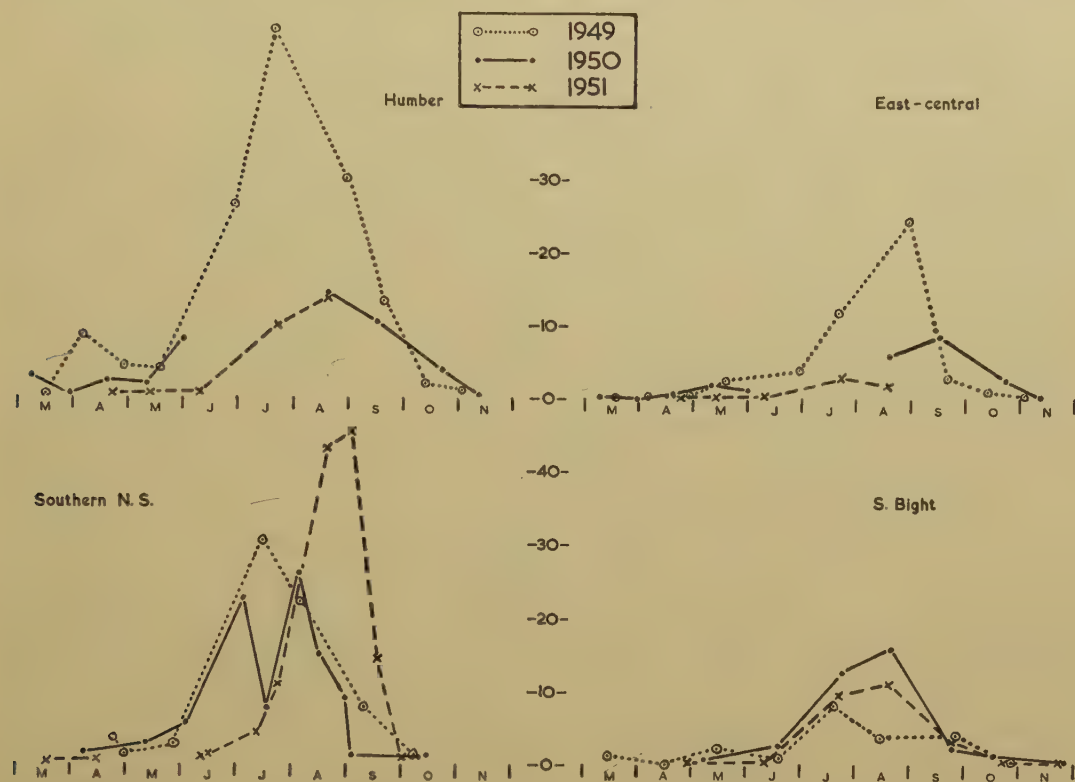
DISTRIBUTION OF SPECIES.

There is one major difference in the nomenclature from that used in the 1947-49 report. Difficulty had been encountered in the naming of the *Callianassa* larvae in the Recorder material (Rees, 1952, p. 170). According to Balss (1926) and Selbie (1914) *C. stebbingi* is the common species in the North Sea, whereas the common larva obtained by the Recorder agrees with the description of the larva assigned to



TEXT-FIG.2.—Charts showing the distribution of decapod larvae, all species combined, in some months of the years 1949 to 1951. Observations from January to June are included in a single chart; roman numerals indicate the months of occurrence of larval concentrations.

C. subterranea. A compromise was adopted whereby the common larva was called *C. stebbingi* (?) and the uncommon larva, which was confined to the Southern Bight, *C. subterranea* (?). Lutze (1938), whose paper had been overlooked in preparing this earlier report, gives *C. subterranea* and *C. helgolandica* Lutze as the North Sea species. He discounted the possibility that *C. stebbingi* occurs in the North Sea but made no comment on the statements by Balss and Selbie that this is the species



TEXT-FIG. 3.—Graphs showing the number of decapod larvae, all species combined, per 10-mile sample of each record in the regions shown in Text-fig. 1. Records taken during the winter months are not included.

occurring there. Lutze also described the larvae of the two species and, on the basis of these descriptions, it is now clear that the common larva, hitherto called *C. stebbingi* (?), is that of *C. subterranea*, and the rare larva, called *C. subterranea* (?), is that of *C. helgolandica*.

Processa edulis.—(Plate XIII.) The observations are, clearly, very compact. Only four specimens were found in 1950, but thirty were obtained in 1951. The larvae were, therefore, unusually abundant in 1951 for only 11 specimens were obtained throughout 1947 to 1949. The larvae were also relatively persistent for they were obtained, more or less in the same place, in three successive records dated August 18 and September 3 and 16.

Processa aequimana.—(Plate XIII.) The distribution in 1950-51 resembles most closely that of 1947 and differs significantly from that of 1948. In 1948 it was *P. aequimana* which was found on the Hull-Bremen route, in 1950 and 1951 *P. edulis*. Eight specimens of this exotic larva were found in 1950, fifteen in 1951.

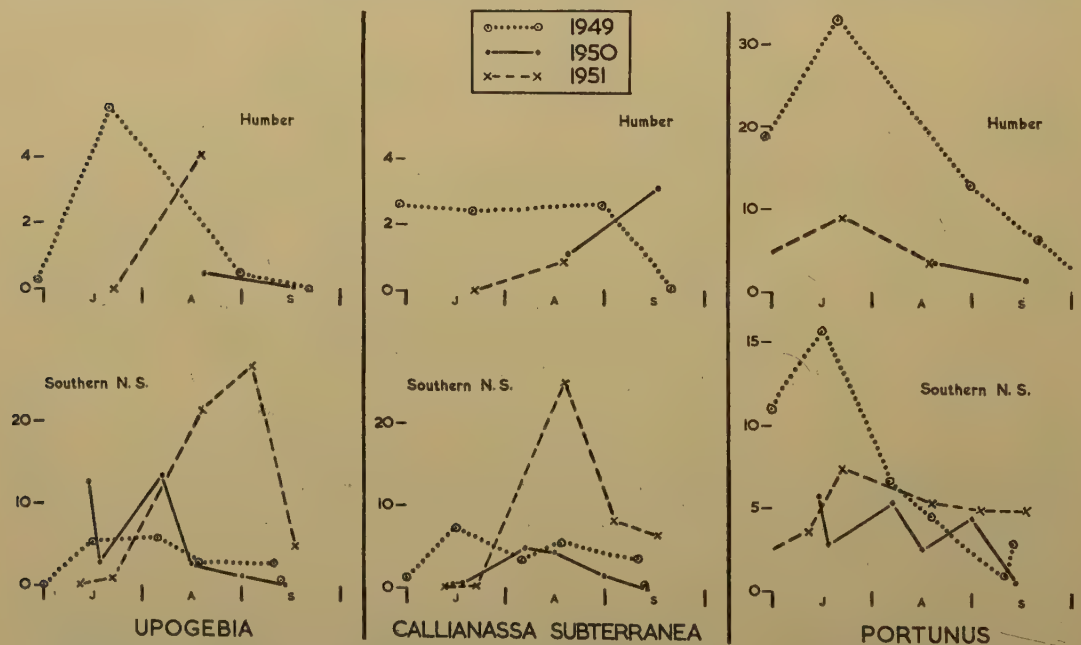
Pontophilus bispinosus.—Only 15 larvae were obtained throughout 1950 and 1951. This is a good example of how the restriction of examined samples affects the results. Previously, the greatest number of larvae were found in October, but no October samples were examined for species in these two years. There is little doubt, however, that larvae of this species were much more numerous in 1948 than in 1950 and 1951.

Upogebia deltaura.—(Plate XIV, Text-fig. 4.) As previously, every specimen was not assigned to its species but it has been confirmed that the very great majority of *Upogebia* larvae were of *U. deltaura*, *U. stellata* being very rare.

Failure to obtain some Hull-Copenhagen records makes a comparison of years in the "Humber" region uncertain. The only clear indication is that appreciable numbers of larvae occurred earlier in 1949 than in 1951. In the "Southern North Sea", also, the main population of 1951 occurred later than in 1949 and 1950, but it was much heavier. The dense and persistent patch in 1951, midway between the Dogger Bank and the Heligoland Bight, is especially noteworthy.

Callianassa subterranea=*C. stebbingi* (?) of Rees (1952).—(Plate XIV, Text-fig. 4.) As in the case of *Upogebia*, *C. subterranea* larvae were more plentiful in 1951 than in 1950 and a persistent patch was sampled midway between the Dogger Bank and Heliogland Bight. One sample in 1951 contained 107 larvae and there were three others with over 50 larvae. The greatest number in any sample from 1947 to 1950 was 31.

Callianassa helgolandica=*C. subterranea* (?) of (Rees) 1952.—Larvae were obtained only on the eastern half of the Hull-Rotterdam record of August, 1951, there being 17 specimens in all.



TEXT-FIG. 4.—Graphs showing the number of larvae of *Upogebia*, *Callianassa subterranea* and *Portunus* per 10-mile sample of each record sampling the "Humber" and "Southern North Sea" regions during July to September.

Galathea spp.—During the period 1947 to 1949 larvae of *G. dispersa* and *G. squamifera* were found chiefly in the north-west North Sea and around the Danish coast. The main concentrations of *G. intermedia* were found off the Humber while *G. strigosa* larvae were very rare. The 1950 and 1951 results agree with these findings, but very few samples north of the Dogger Bank were examined for species. The distributions of the larvae of *G. intermedia* are shown in Plate XIII.

Porcellana longicornis.—(Plate XIII.) Larvae of this species were much more numerous in 1949 than in 1947 and 1948 (Rees, 1952). In 1950 the larvae were even more numerous but fell back to approximately the 1948 level in 1951. The almost complete restriction to British coastal waters is clear.

Eupagurus bernhardus.—(Plate XIII.) The larvae, which constituted so important a part of the 1947 decapod community, were uncommon in 1950 and might even be considered rare in 1951. As previously, the centre of abundance was along the southern edge of the Dogger Bank.

Corystes cassivelaunus.—(Plate XIII.) Larvae of this species occur chiefly in May and June (Rees, 1952). Since so few 1950 and 1951 samples of this period were examined for species, the number of *Corystes* larvae observed was very low.

Portunus.—(Plate XIV, Text-fig. 4.) Comparing the distributions with those for 1949 (Rees, 1952), it can be seen that *Portunus* larvae had declined greatly in numbers in 1950 and 1951. It is unfortunate that there was no Hull-Copenhagen record between June 1st and August 18th, 1950, so that no samples were taken along this route when *Portunus* larvae were, doubtless, at their greatest abundance. However, the decline is clear when the Leith-Copenhagen and Hull-Bremen routes of each year are compared. In both 1950 and 1951 *Portunus* larvae were less numerous than *Upogebia* (Plate XIV) whereas, in 1949, six times as many *Portunus* as *Upogebia* larvae were obtained. The decline, however, did not reduce the numbers as low as the 1947 level.

Thia polita.—(Plate XIII.) More larvae were found in 1951 than over the whole period of 1947 to 1949. 1950 appears to have been an average year for the species. Not only were the larvae restricted in space but also in time for 90% of the larvae were found in August.

Cancer pagurus.—(Plate XIII.) In general, we may recognize three main centres for the larvae, one off the Forth, another between the Humber and Dogger Bank, and a third just west of the Heligoland Bight, but a little east of the main *Upogebia* patch in this part. The first and second centres may, of course, be part of a continuous distribution. In 1949 high numbers were obtained off the Skaw and between the Dogger and the Danish coast. Such high numbers were not obtained here in 1950 and 1951.

DISCUSSION.

In order to compare the relative abundance of decapod larvae over the five years which have now been studied, it is necessary to adjust the results for 1947–1949 to allow for the reduction in detail available for 1950 and 1951. It will be recalled that every 10-mile sample taken in 1947 and 1948 was analysed for larvae whereas only alternate samples were analysed in 1949 to 1951. The first adjustment is to disregard half the samples of 1947–48 and use only the alternate ones. The effective number of samples taken in each year becomes as given in line (a) of Table I. A measure of relative abundance can be gained by finding the proportion of these samples which contained 12 or more (b) and 50 or more larvae (c). Because, in the 1950 and 1951 material, larvae were identified and accurately counted only in those samples containing 12 or more larvae, the second adjustment is to assume that larvae were identified and counted only in such samples of 1947 to 1949. In this way, the comparable number of larvae examined in each year becomes as given in

line (d), from which the suitably adjusted average number of larvae per alternate sample can be derived (e).

TABLE I.—*The Relative Abundance of Larvae from Year to Year.*

	1947	1948	1949	1950	1951
(a) Total number of samples	708	904	804	765	751
(b) % of samples containing 12 or more larvae	3	8	10	9	7
(c) % of samples containing 50 or more larvae	0.3	0.7	2.0	0.5	1.5
(d) Number of larvae examined	440	1932	2552	1534	2003
(e) Average number of larvae per sample	0.6	2.1	3.2	2.0	2.7

It is clear from these values that larvae were very scarce in 1947, when only 3% of samples contained 12 or more larvae and the average number per sample was only 0.6, and that larvae were most abundant in 1949, with corresponding values of 10% and 3.2. The 1948 and 1950 populations may be regarded as moderate. In 1951 the percentage of samples containing 12 or more larvae was lower (7%), but the percentage of samples containing 50 or more (1.5%) and the average per sample (2.7) were high. These results reflect the fact that the very abundant, but restricted, concentration just outside the Heligoland Bight more than compensated for the notable scarcity in the period April to June (Text-fig. 3).

In a year when decapod larvae were exceptionally abundant, 1938, 14% of all 10-mile samples contained 12 or more larvae.

In order to consider the relative numbers of larvae of various species from year to year, the value used is the total identified number of larvae of each species, divided by the number of samples containing 12 or more decapod larvae, that is of re-examined samples. The values are shown in the vertical histograms of Text-fig. 5. Here we can recognize the relatively great abundance of *Upogebia deltaura* and *Callianassa subterranea* in 1951, of *Porcellana longicornis* in 1950, of *Portunus* spp. in 1949 and of *Eupagurus bernhardus* and *Cancer pagurus* in 1947.

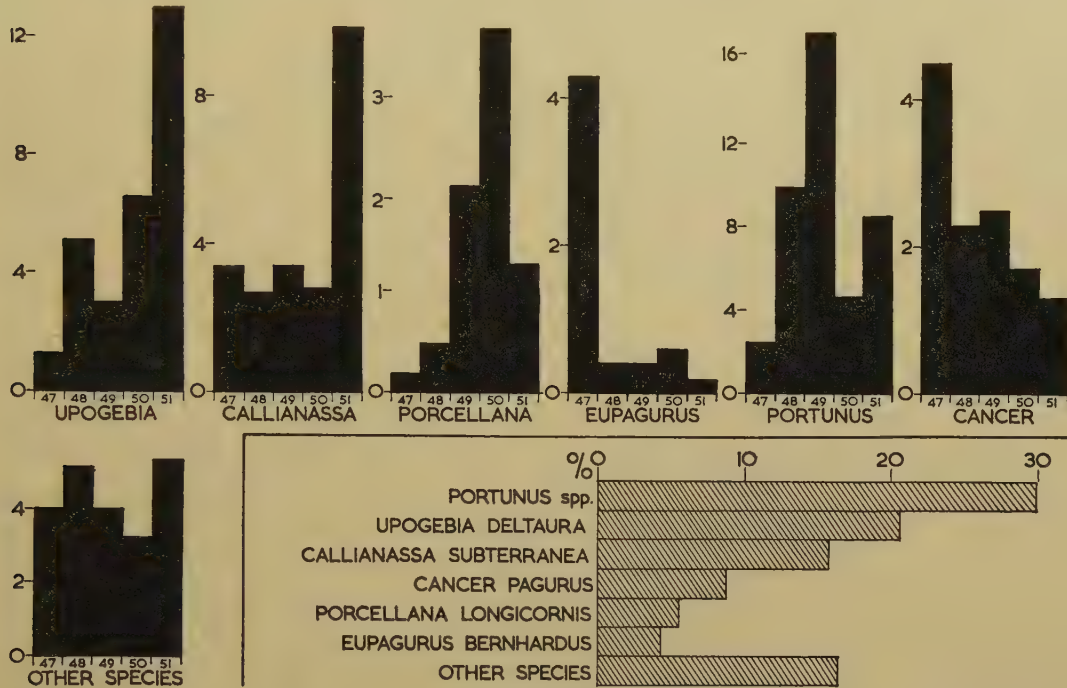
Of the less common species which have shown yearly fluctuations we may note, in particular, the abundance of *Pontophilus bispinosus* in 1948 (Rees, 1952) and of *Processa edulis* and *Thia polita* in 1951.

The numbers of decapod larvae found in 1938 (Marshall, 1948) were so exceptionally high that some samples have been examined to determine which species contributed to the high numbers. Two species were responsible for the great concentration just outside the Heligoland Bight, *Callianassa subterranea* and *Upogebia deltaura*, especially the former. There were several samples containing many more than 300 *Callianassa* larvae; the greatest number in any sample obtained in 1947 to 1951 was 107 (p. 74). One sample from the concentration near the East Anglian coast in July, 1938, contained approximately 800 *Porcellana longicornis* and 350 *Pilumnus hirtellus*.

The decapod larvae are, of course, far from being unique in showing an unusual abundance of one or two species in each year. Similar examples have been noted amongst the lamellibranch and echinoderm larvae (Rees, 1954a and b) and there are

many examples amongst the permanent plankton forms. Such occurrences, when they have been fully recognized and can be considered in total, should prove a most valuable means of interpreting the interaction between plankton and environment.

The horizontal histograms in Text-fig. 5 show the percentage composition of the decapod population over the five years, using the estimates that go to making up the other part of this text-figure. Because the population of *Portunus* is made up



TEXT-FIG. 5.—The black histograms show the relative abundance of some species in each year from 1947 to 1951. The vertical scale indicates the number per 10-mile sample, the samples being restricted, as explained in the text, so as to make the values for each year suitably comparable. The hatched histograms illustrate the percentage composition of decapod larvae taken from 1947 to 1951.

of a number of species (Rees, 1952, p. 179), it is probable that *Upogebia deltaura* and *Callianassa subterranea* are the two most common species of decapod larvae in the North Sea, as at present revealed by the Recorder collections.

Separate charts have previously been given to show the general distribution of very high concentrations of larvae, and these have shown marked differences. For decapods (Rees, 1952) and echinoderms (Rees, 1954b) the charts were, however, mainly determined by the distributions of 1938, partly because of the much greater extent of Recorder sampling and partly because the numbers of these larvae were exceptionally high during this period. This possible bias is avoided in Text-fig. 6



TEXT-FIG. 6.—Charts showing the distribution of 10-mile samples containing high numbers of decapod, echinoderm and lamellibranch larvae over the period 1947 to 1951. The chart in the lower right corner shows the percentage number of observations of each group falling into four arbitrary areas of the North Sea; only those observations shown in the remainder of the text-figure are taken into account.

by giving the distribution of samples containing high numbers of the three groups for the years 1947 to 1951 only. The lower limit of 36 per sample for decapods has been chosen so as to give about the same number of observations as for echinoderms and lamellibranchs.

The chart in the bottom right shows the North Sea arbitrarily divided into four areas. The number of observations of each group in each area is given in the chart as the percentage of all observations of the group. It can be seen that more than half the observations for decapod larvae fall in the south-west area, and of lamellibranch larvae in the north-east area and very nearly half of echinoderm larvae in the south-east. The great majority of lamellibranch observations fall in the two northern areas (85%) and of decapod larvae in the two southern (79%). It should be made clear that the values given in Text-fig. 6 are to be regarded as relative to each other. No allowance has been made for differences in the total number of samples taken in each area.

It may be desirable to qualify the values for decapod larvae. Whilst twice as many observations of over 36 larvae were obtained in the south-west as in the south-east, there were six observations in the west with over 100 larvae as compared with five in the east. In itself this is not, of course, significant but it does fit in with the results for the two southern areas over the combined years 1932 to 1937. For this earlier period the higher the concentration level selected the higher the proportion of observations which fall in the east. Of samples with over 25 larvae 61% fell in the west, 39% in the east; with over 50 larvae 50% each in west and east; with over 100 larvae 31% in the west, 69% in the east. A possible explanation is that the species which reach the greatest population densities are *Upogebia deltaura* and *Callianassa subterranea* and these are mainly centred in the south-east.

The number of larvae in the surface waters is, of course, not necessarily an indication of the number of spawning adults immediately below. The planktonic larvae are carried, in moving water, varying distances and directions from the spawning grounds, as witnessed by the transport of immense numbers of *Mytilus edulis* larvae for at least 200 miles (Rees, 1954a). Nevertheless, the differences brought out in Text-fig. 6 do suggest that the main spawning populations of decapods, of echinoderms and of lamellibranchs are differently distributed and do not coincide.

SUMMARY.

1 The distribution of decapod larvae in 1950 and 1951 is dealt with on the same lines as for 1947 to 1949 (Rees, 1952) but with much reduced detail. Only the common species and those of particular interest are included.

2. Decapod larvae were less numerous in the Humber region than in 1949. Dense concentrations were found in the southern North Sea in 1951.

3. A comparison between the years 1947 to 1951 shows that larvae were, overall, very scarce in 1947 and most abundant in 1949.

4. The names *Callianassa stebbingi* (?) and *C. subterranea* (?) used in the previous report (Rees, 1952) have been amended to *C. subterranea* and *C. helgolandica* Lutze respectively.

5. *Porcellana longicornis* was relatively very numerous in 1950 and *Upogebia deltaura*, *Callianassa subterranea*, *Processa edulis* and *Thia polita* in 1951.

6. Check analyses have shown that *Upogebia deltaura* and *Callianassa subterranea* were exceptionally abundant in 1938.

7. *Upogebia deltaura* and *Callianassa subterranea* have been, overall, the most common species of larvae obtained in the North Sea.

8. A comparison of the distribution of larvae of decapods, echinoderms and lamellibranchs suggests that the main spawning populations of these three groups are differently distributed and do not coincide.

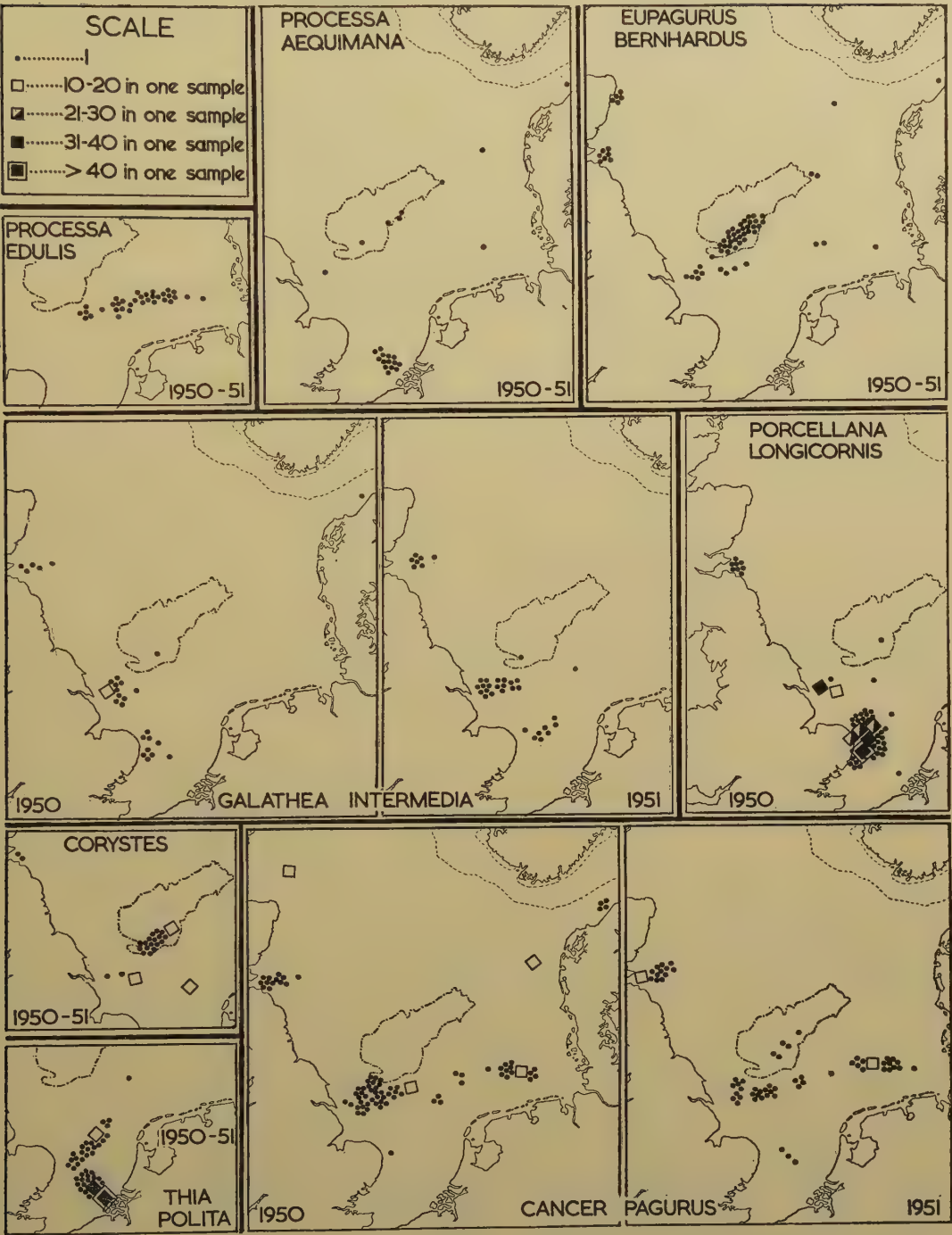
REFERENCES.

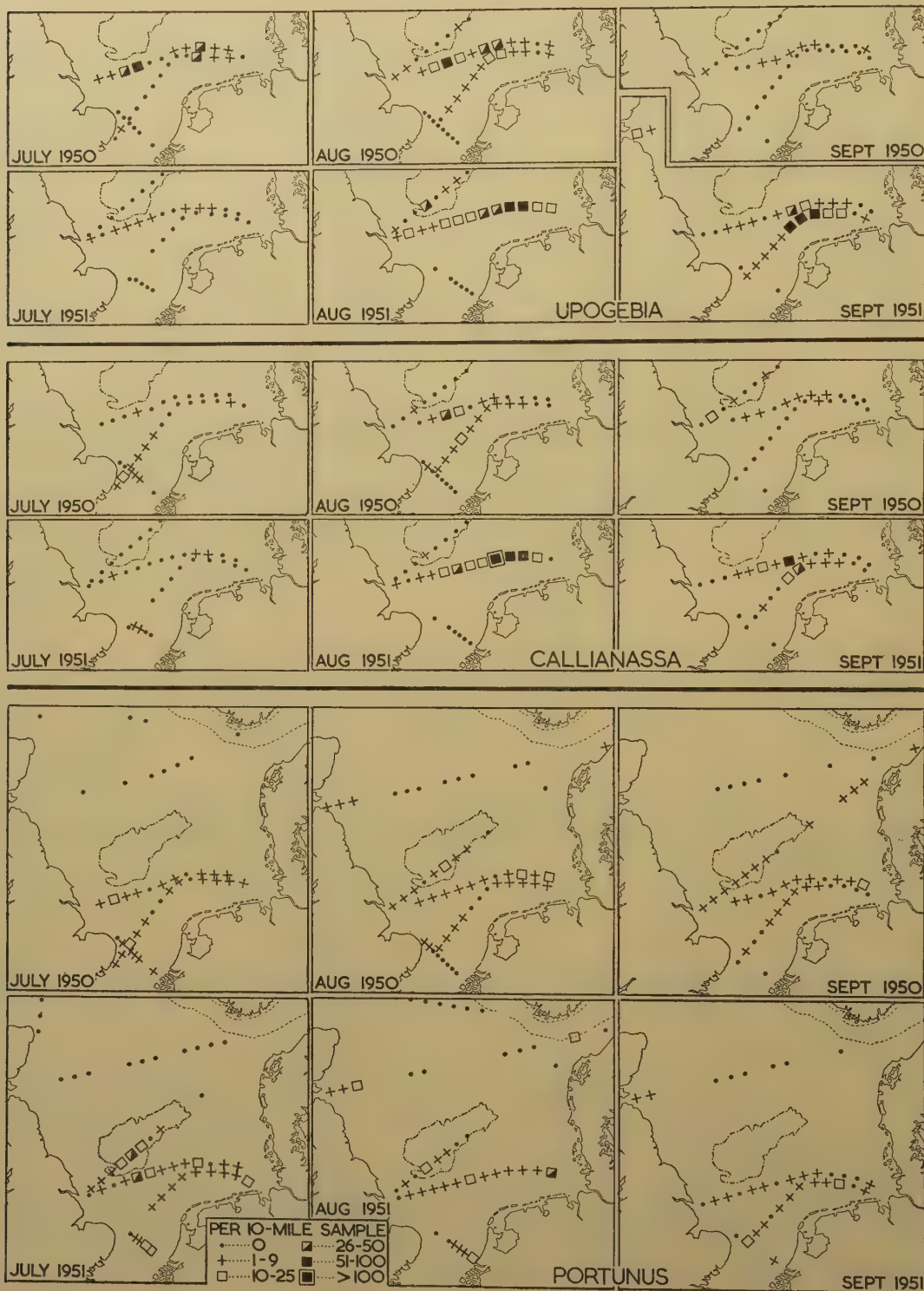
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EXPLANATIONS OF PLATES.

Plate XIII.—Charts showing the distribution of some species of decapod larvae in the North Sea during 1950 and 1951, according to the scale in the upper left corner.

Plate XIV.—Charts showing the distribution in each month from July to September of 1950 and 1951 of larvae of *Upogebia*, *Callianassa subterranea* and *Portunus*. The scale is given on the bottom.





CONTINUOUS PLANKTON RECORDS: LIST OF RECORDS, 1953—54

BY

K. M. RAE, O.B.E., B.Sc.

THE Plankton Recorder Survey of the North Sea and the eastern Atlantic was continued during 1953 and 1954 on a scale very similar to previous years. This was only possible, of course, through the unfailing co-operation of the personnel of the many ships which towed Hardy Continuous Plankton Recorders on their voyages. Again, the Association wishes to express its thanks to the owners, masters and crews and also to the other personnel of the companies and organizations concerned; without their generous assistance the programme could not have been accomplished. The following vessels participated:

- | | | |
|--|---|---|
| S.S. "Harrogate" | } | Associated Humber Lines Ltd. |
| S.S. "Melrose Abbey" | | |
| S.S. "Gothland" | } | James Currie & Co. Ltd. |
| S.S. "Horsa" | | |
| S.S. "Borodino" | } | Ellerman's Wilson Line Ltd. |
| S.S. "Leo" | | |
| S.S. "St. Clair"—The North of Scotland and Orkney and Shetland Steam Navigation Co. Ltd. | | |
| S.S. "Sarpfoss"—Thor Thoreson & Co. Ltd. | | |
| S.S. "Tjaldur"—Faeroes Steamships Co. Ltd. | | |
| O.W.S. "Weather Explorer" | } | Weather Ships Service, Air Ministry,
London. |
| O.W.S. "Weather Observer" | | |
| O.W.S. "Weather Recorder" | | |
| O.W.S. "Weather Watcher" | | |
| O.W.S. "Polarfront I"—The Norwegian Committee on Weather Station
"M", Oslo. | | |
| O.W.S. "Cumulus" | } | The Royal Netherlands Meteorological Institute,
de Bilt. |
| O.W.S. "Cirrus" | | |

In the later half of 1954 some unusual routes were introduced to the survey. In the main these arose from the re-siting of the international weather stations and temporary changes in the responsibility for the tours of duty on them. For some months the Dutch weather ships watched on Station M which had previously been the responsibility of Norway. This led to a slight westerly shift in the course of the T route and also enabled some north-south tows in the North Sea on a new P route. In the meantime, the Norwegian ships took turns on Station A, south-west of Iceland, and the V route was so taken north of Faeroes. At the end of 1954 the British ships started tours on Station A and it is hoped that by providing them with extra Recorders we may be able to obtain samples further west into northern Atlantic than previously; the short U route in December was the first attempt at this.

In July, 1954, we were very pleased to be able to start a new route, Q, which promises to be most valuable to the survey. The Faeroes Steamship Company put their S.S. "Tjaldur" at our disposal. She trades between Thorshaven and Copenhagen, occasionally calling at Lerwick during the summer season.

Previous station lists or summaries of records have been published from time to time in the 'Bulletins': that for 1931-37 in Vol. I, No. 2; that for 1938-39 in Vol. II, No. 7; that for 1946-49 in Vol. III, No. 21; and that for 1950-52 in Vol. IV, No. 25. The arrangement here is just the same as in the two more recent summaries. Each route has its code letter and the records taken on it have been numbered serially since it was started. For example, 76X was the 76th tow taken on route X, which runs from the Clyde towards weather station "I"; 45G, the 45th tow between the Thames estuary and the Skagerrak; etc. Table I comprises a list of the records arranged chronologically, month by month. The date or dates on which each record was taken are given together with the *ratio*, or the total mileage towed divided by the number of 2-inch divisions of filtering silk which were wound through the machine during the tow. Although it has been included for the sake of consistency, this ratio is not of general importance. In the sub-sampling technique used for estimating the quantity of plankton caught an arbitrary ratio of 5 is adopted. It is assumed, for convenience, that the plankton from any 10-mile sample was deposited on an area of silk which measures 4 inches by 4 in. If, in fact, the ratio was less than 5 miles of tow for each 2 in. of filtering silk, then the plankton in each sample is spread over a bigger area and the estimate tends to be low. Correspondingly, if the ratio is greater than 5, the estimate is high. Details of the method used and the significance of the ratio are given in 'Bulletin' No. 21.

Plates XV-XVIII comprise a series of charts, each representing a single month. They illustrate the course over which each record was taken, the direction of tow and those parts sampled by day and by night. Individual records can be identified by their code letters and serial numbers.

Each autumn a few records additional to the normal programme were taken on the Forth to Skagerrak route and only certain species were counted on them. Such records are marked with an *asterisk* in Table I and are shown on the charts merely by their serial numbers, thus "+ 134K".

TABLE I.—*A List of the Records shown in Plates XV–XVIII arranged by Months.*

The serial number and code letter of each Record is followed by the date or dates on which the tow was taken. The Records marked with an *asterisk* were taken for some special purpose and were in addition to the normal survey: the plankton caught on them has not been fully analysed. The final figure in each entry gives the ratio of miles per division, *i.e.*, the total mileage towed divided by the number of 2-in. divisions of silk that crossed the water tunnel.

1953			1953 (contd.)			1953 (contd.)		
Record.	Date.	Ratio.	Record.	Date.	Ratio.	Record.	Date.	Ratio.
<i>January</i>			<i>April</i>			<i>July</i>		
76X	8/9	4.5	49M	2/3	5.4	126K	3/5	5.5
45G	10/11	4.7	79X	2/4	5.2	51M	10/11	6.7
110A	10/11	5.1	80W	3/5	4.9	28J	15/17	4.8
55V	12/14	4.6	112A	4/5	5.0	84X	16/17	5.2
77W	13/15	5.0	123K	11/12	5.0	127K	17/19	5.4
8H	15/17	6.5	174C	11/12	5.3	177C	18/19	5.7
171C	16/18	5.0	193B	11/12	5.0	198R	19	4.4
190B	17/18	5.0	195R	19	4.9	196B	19/20	4.9
192R	18	5.0	23J	22/24	5.5	57V	20/22	6.9
119K	24/25	4.6	80X	25/27	5.3	115A	25/26	5.4
44T	27/29	5.5	81W	25/26	5.0			
			<i>May</i>			<i>August</i>		
<i>February</i>			47T	1/2	5.9	128K	31/1	5.0
9H	8/9	5.8	81X	14/15	5.3	85X	6/7	4.9
172C	14/15	4.9	82W	14/16	5.6	84W	6/8	5.9
191B	14/15	4.9	124K	16/18	5.3	52M	7/8	5.8
193R	15	4.2	24J	16/18	5.3	29J	8/10	4.6
77X	19/20	4.8	82X	18/20	4.9	178C	14/16	5.1
78W	19/21	5.2	175C	23/24	4.7	197B	16/17	5.1
10H	27/1	5.9	194B	23/24	5.2	199R	16	4.8
45T	27/28	5.0	196R	23/24	4.9	58V	25/27	5.1
121K	27/1	5.4	50M	28/30	6.3	30J	27/29	5.0
111A	28/1	4.8	113A	30/31	5.1	85W	29/31	4.9
			48T	30/1	6.0	86X	29/30	4.5
						51T	31/1	5.2
<i>March</i>			<i>June</i>			<i>September</i>		
48M	8/9	5.8	25J	3/5	4.8	129K	5/7	5.7
78X	13/15	4.9	125K	20/21	5.3	116A	5/6	4.7
122K	14/15	5.3	176C	20/21	5.0	179C	11/12	4.6
79W	14/16	5.4	195B	20/21	5.4	200R	13	4.4
173C	14/15	4.7	197R	21	4.7	87X	17/19	4.8
192B	14/15	4.6	56V	23/25	6.9	86W	18/19	5.4
11H	22/24	4.4	83W	25/27	5.2	130K	19/21	5.6
46T	30/1	6.7	27J	28/30	4.6	198B	19/20	5.0
			49T	30/1	6.1	52T	30/1	6.7

TABLE I—*contd.*

1953 (<i>contd.</i>)			1954 (<i>contd.</i>)			1954 (<i>contd.</i>)		
Record.	Date.	Ratio.	Record.	Date.	Ratio.	Record.	Date.	Ratio.
<i>October</i>			<i>February</i>			<i>June</i>		
131K	3/5	4.7	93X	14/15	5.3	150K	5/7	5.2
117A	3/4	4.8	89W	14/16	4.3	120A	12/13	4.3
88X	10/11	4.7	142K	24/26	5.2	51G	15/16	4.4
201R	11	4.4	58T	26/27	5.0	33J	16/17	5.1
87W	13/14	5.7	183C	27/28	5.3	97X	18/20	4.8
53T	16/17	6.1	205R	28	4.8	187C	18/20	5.1
47G	17	5.3				151K	19/21	4.7
132K	17/18	4.7				68V	25/27	5.7
133K	24/26	4.8				52G	26/27	5.2
54T	30/31	5.2						
<i>November</i>			<i>March</i>			<i>July</i>		
53M	5/6	7.7	64V	2/4	5.7	205B	4/5	4.7
134K*	6/8	4.4	143K	12/14	5.0	93W	7/9	5.1
48G	13/14	5.0	12H	18/21	4.7	98X	8/10	5.5
135K	21/22	4.7	90W	25/27	5.1	34J	10/11	5.2
200B	22/23	4.7	94X	26/28	4.7	153K	16/18	4.4
55T	29/30	4.9	145K	26/28	4.7	188C	17/18	5.2
			184C	27/28	5.0	61T	21/23	5.0
			59T	30/1	4.9	121A	24/25	4.3
<i>December</i>			<i>April</i>			208R	25	4.6
136K*	5/6	4.5				57M	28/30	7.1
49G	11	5.6	146K	9/11	4.7	154K	30/1	5.4
89X	15/16	5.2	203B	11	4.5	1Q	31/1	3.9
54M	18/19	6.9	95X	17/18	4.5			
137K	19/20	4.2	91W	17/19	5.7			
118A	19/20	5.0	147K	23/25	4.9			
201B	19/20	4.9	185C	23/25	5.1			
203R	20	5.2	206R	25	4.7			
56T	27/29	5.9						
62V	30/1	5.4						
90X	31/2	6.0						
<i>1954</i>			<i>May</i>			<i>August</i>		
<i>January</i>			66V	4/6	5.3	94W	1/3	4.8
138K*	2	4.8	31J	5/7	5.0	69V	2/4	6.1
139K	16/18	4.8	148K	7/9	5.1	2Q	5	3.9
204R	17	5.2	204B	15/16	4.4	155K*	7/9	4.6
91X	21/22	5.3	207R	16	4.6	62T	13/15	5.3
88W	21/23	4.8	56M	16/17	5.5	156K	13/15	4.9
92X	23/25	4.9	149K	21/23	4.6	189C	14/15	5.1
182C	24/25	5.3	96X	27/29	5.1	122A	14/15	4.5
202B	24	4.4	92W	28/29	5.1	209R	15	4.4
63V	25/26	5.2	119A	29/30	4.2	2P	16/17	5.0
50G	25/26	5.2	32J	29/31	5.2	95W	19/20	5.2
140K*	29/31	5.1	186C	30/31	5.2	99X	19/20	4.9
			67V	31/2	5.1	3Q	27/28	5.0
						157K*	27/29	5.1

TABLE I—*contd.*

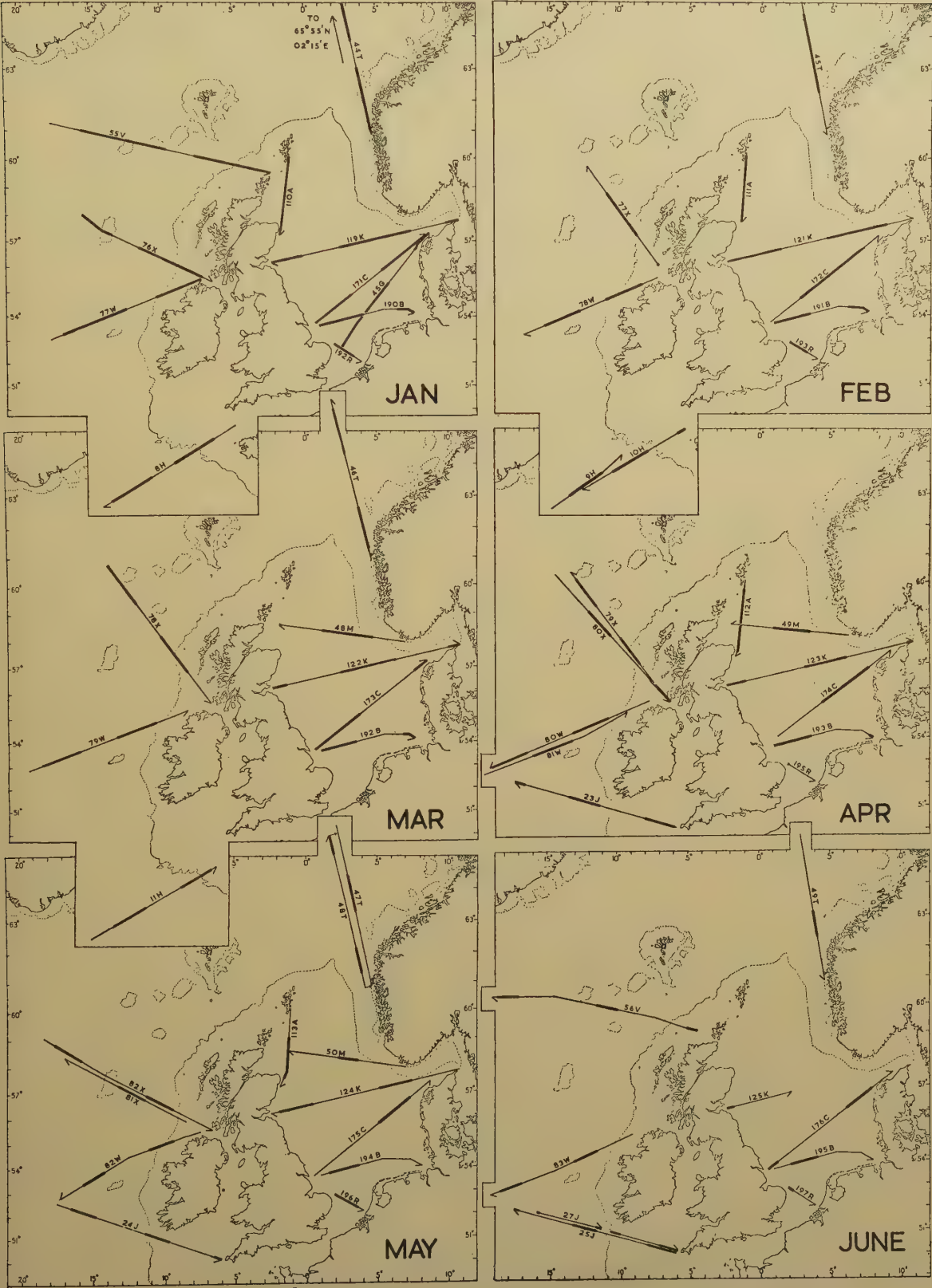
1954 (<i>contd.</i>)			1954 (<i>contd.</i>)			1954 (<i>contd.</i>)		
Record.	Date.	Ratio.	Record.	Date.	Ratio.	Record.	Date.	Ratio.
<i>September</i>			<i>October</i>			<i>November</i>		
63T	4/7	5.1	4Q	2/3	5.0	162K*	5/7	5.6
206B	5	4.6	71V	3/5	7.6	191C	6/7	4.9
3P	8/10	5.6	4P	3/5	5.5	98W	13/15	5.2
158K	11/12	5.0	160K	9/10	5.8	163K*	14/16	5.5
100X	11/12	4.7	211R	10	4.9	212R	18	5.4
190C	11/12	5.2	207B	16/17	5.3	164K	19/20	5.5
210R	12	4.2	97W	21/23	5.8	6P	20/21	5.2
123A	18/19	5.4	101X	21/23	6.7			
159K*	25/26	5.7	161K*	23/24	5.4	<i>December</i>		
64T	30/2	4.9	65T	24/26	4.8	165K	3/4	5.7
			72V	25/27	6.4	99W	5/6	4.9
			5P	28/29	4.9	67T	11/13	5.3
			124A	30/31	5.5	213R	16	4.1
						192C	18	4.7
						166K*	25/26	5.5
						1U	28/29	4.9

EXPLANATION OF PLATES XV TO XVIII.

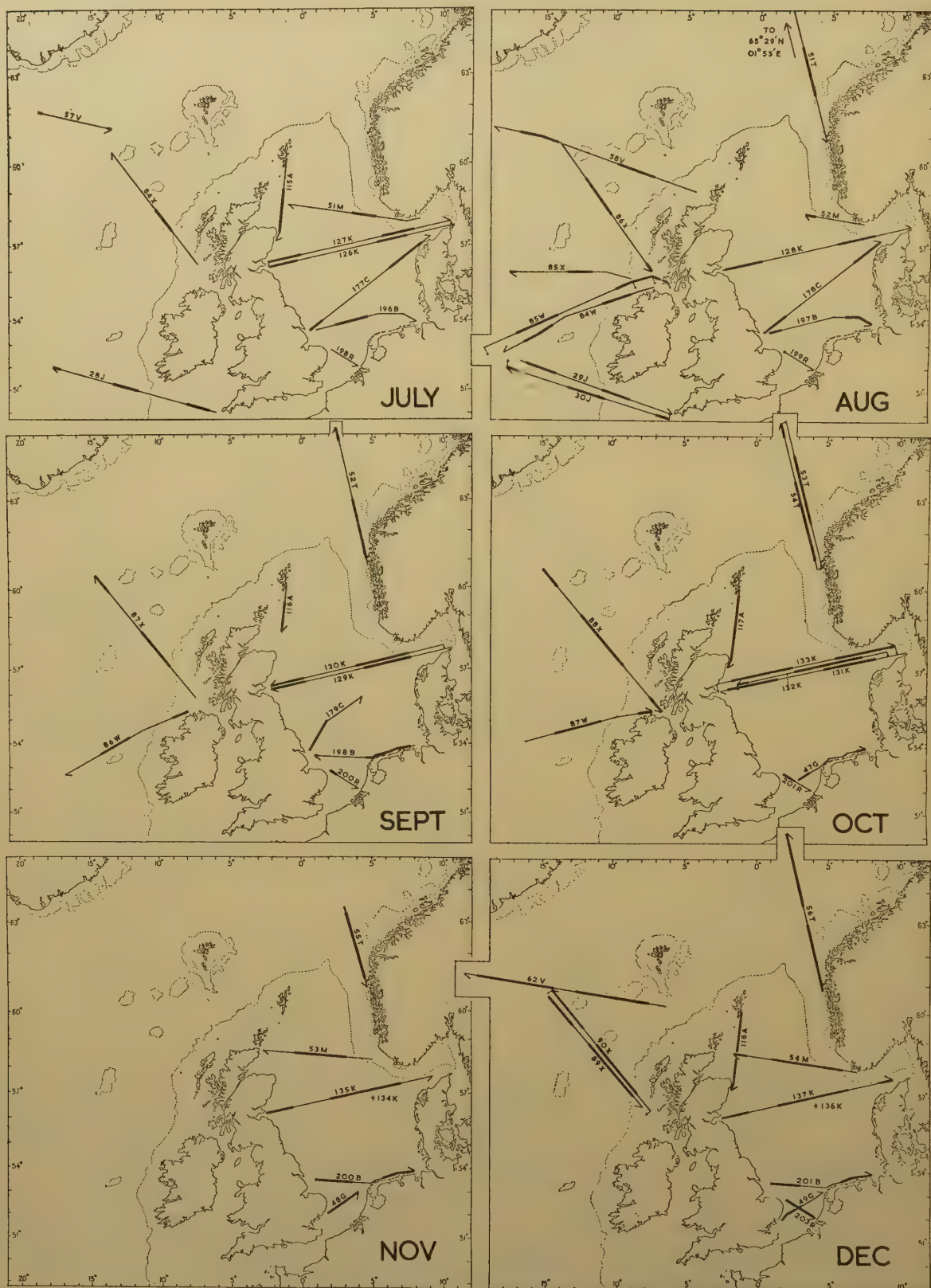
Monthly charts of the Recorder tows taken between January, 1953, and December, 1954. The position and extent of each record is shown by a line against which is placed its serial number and route letter. The date, or dates, on which each tow was made can be found by reference to Table I (p. 83). The half arrow-head at one end of the line indicates the direction of the tow, and those parts of a record taken between sunset and sunrise are shown by a thicker line than those taken during the day-time.

Here and there, when more than one record was taken over the same route in a month, it has been necessary to displace a record on the chart; then arrows at each end of the line indicate its correct position.

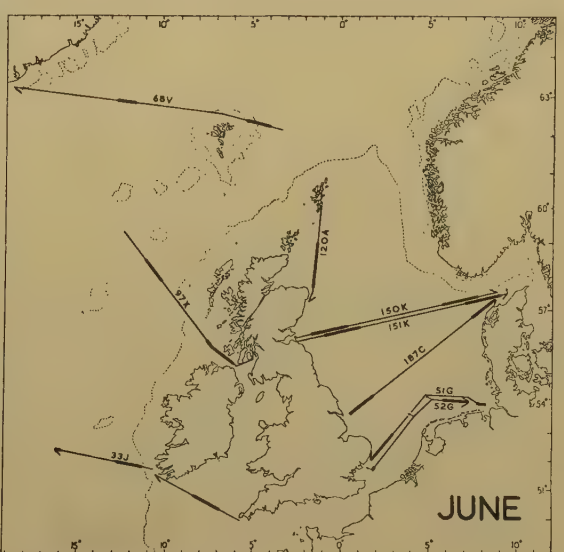
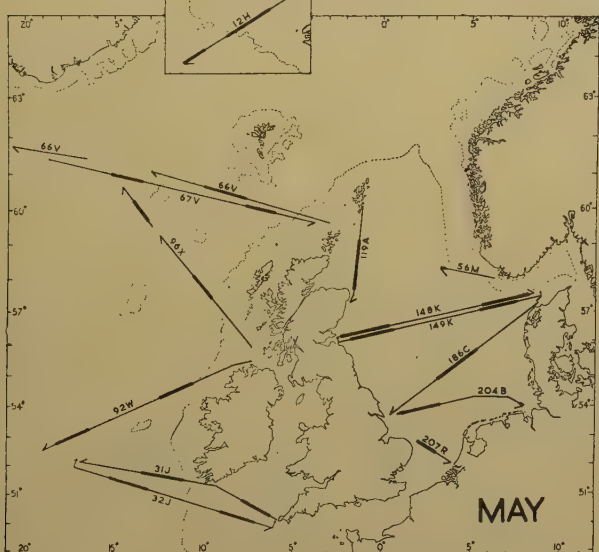
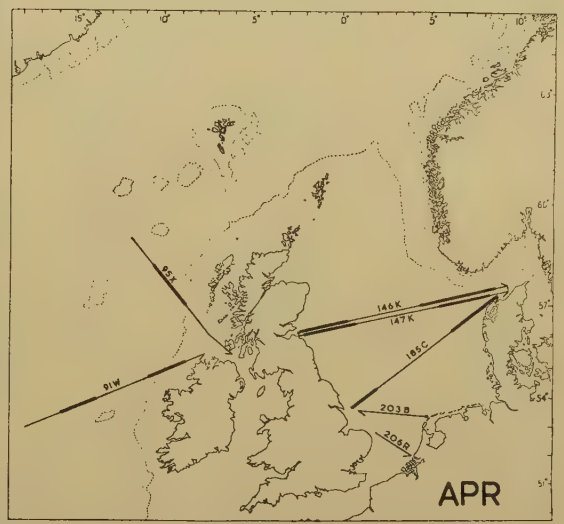
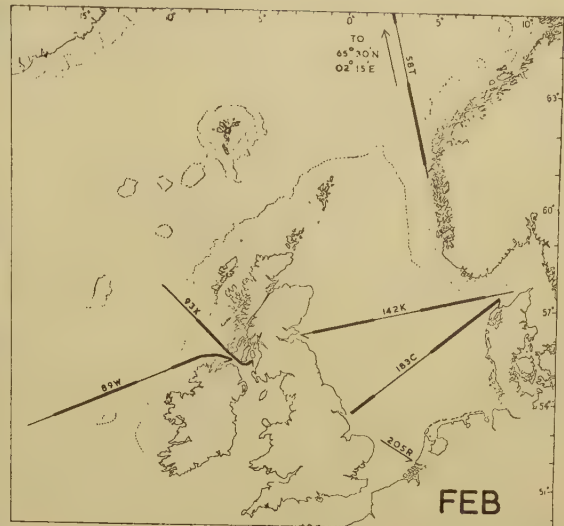
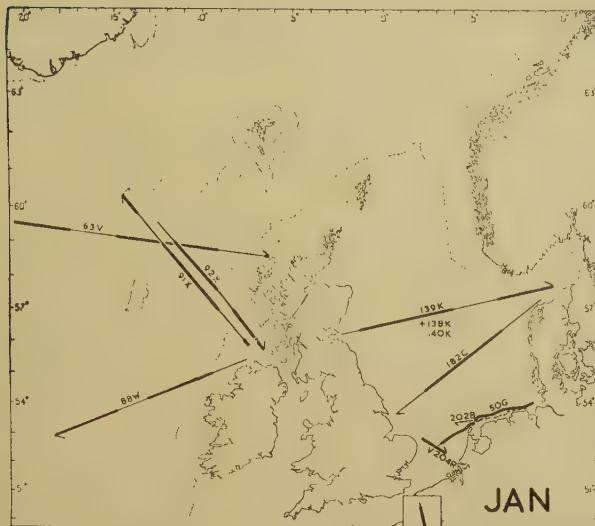
Certain records, on which the plankton has not been fully analysed, are not illustrated; they are shown merely by their serial numbers thus— + 134K.



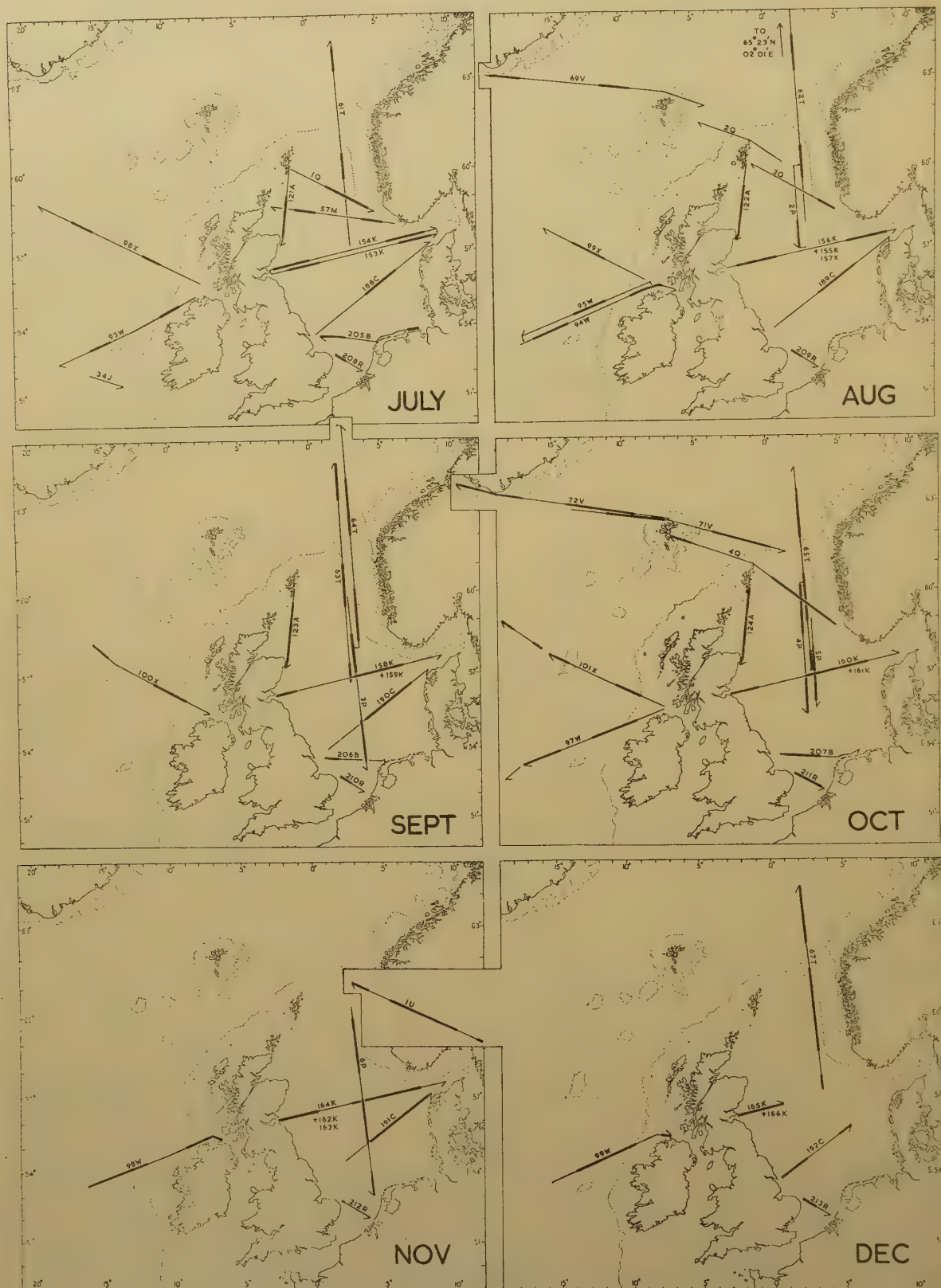
Plankton Recorder lines, January to June, 1953



Plankton Recorder lines, July to December, 1953



Plankton Recorder lines, January to June, 1954



Plankton Recorder lines, July to December, 1954

THE PLANKTON IN THE IRISH SEA, 1951 AND 1952.

BY

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INTRODUCTION.

EARLIER 'Bulletins' on the results of the Plankton Recorder Surveys of the North Sea give several examples of clear correlations between the fluctuating pattern of distribution of many organisms and the distribution and movements of water masses. A previous attempt to obtain a general picture of plankton distribution in the Irish Sea (Williamson, 1952) suggested that equally clear correlations exist between planktonic and hydrographic features in this area, although the correlations are in many cases not those which would have been

predicted simply by analogy with the North Sea. These preliminary surveys of Irish Sea plankton were restricted to the two years 1949 and 1950, and, especially in 1949, were over a very limited area. It remained to test whether these correlations were regular annual features, and in order to find out the extent of the water-masses a larger survey was required. The surveys of 1951 and 1952 were therefore undertaken. The analysis of the plankton samples was extended to include decapod larvae and a fuller identification of euphausiid larvae and Cladocera.

As no further surveys on these lines are contemplated, and as future plankton work in the Irish Sea is being planned on the basis of the present results, it is considered desirable to publish these in some detail.

HYDROGRAPHICAL BACKGROUND.

The water-movements of the Irish Sea are dominated by the tidal currents. In most of the area extending westward and south-westward from the Isle of Man to the Irish coast these currents never attain one knot, but in most of the remainder of the region this speed is exceeded at each ebb and flow, and speeds of three knots are exceeded at spring tides off the Mull of Galloway, off both the north and south of the Isle of Man and off the Anglesey coast (Admiralty, 1943). Apart from some local instances in coastal regions (e.g. Orton, 1937) there is no evidence of tidal swirls which might concentrate plankton in any parts of the Irish Sea, but plankton distribution in much of the area is probably affected by both horizontal and vertical mixing resulting from the tidal currents.

In addition to the tides there is evidence of non-oscillatory currents in the Irish Sea which, in spite of their relative weakness, might be expected to exercise an appreciable effect on plankton distribution. Evidence of these currents comes from salinity and temperature observations covering nearly 50 years, several drift-bottle experiments and some current-meter observations at the Skumlartin Light-Vessel (see Text-fig. 1). (In addition to the references given below, see those given by Lewis, 1934). From this work it is evident that the main non-tidal current of the Irish Sea flows from south to north and tends to curve to the east of the Isle of Man; this easterly curve is most pronounced in spring and least in autumn. There is evidence from salinities that the flow is strongest in spring and weakest in autumn (Bassett, 1910; Daniel, 1930), but Bowden (1950) regards this as not entirely conclusive and comments on the desirability of obtaining confirmation from some other source.

There has been no direct measurement of the rate of flow of this north-going current. Estimates from salinity distribution have given mean values of the flow through St. George's Channel of about 1 mile per day along the axis of the isohalines (Proudman, 1948) and about 0.16 miles per day for the mean current across the Holyhead-Dublin section (Bowden, 1950). The flow along the main axis of the current is the more relevant in considering the transport of planktonic organisms. There has been no estimation of the extent of seasonal or other

variations in the rate of flow. This current brings relatively high salinity water into the area, and salinities in the southern Irish Sea and at the north end of St. George's Channel have been used as an indication of its relative strength (Bassett, 1909, 1910; Daniel, 1930). Bowden (1950), however, has emphasized that these salinities are also affected by the salinity of the water which entered the southern end of St. George's Channel at some earlier but unknown period and by rainfall, evaporation and run-off from the land, and that it is not possible to distinguish fully the effects of these factors in this area. Great caution is therefore



TEXT-FIG. 1.—The Irish Sea, showing depths in fathoms and localities referred to in the text.

necessary in their interpretation, but salinities provide the only available non-biological indication of the strength of the north-going current in 1951 and 1952. Regular observations of surface salinity are made at seven stations in the area by the Oceanography Department of Liverpool University, who have kindly supplied the figures for the periods of the plankton surveys. Mean values for each of these periods are shown in Plates XIX and XX.

The water entering the south of the Irish Sea in May 1952 was of rather higher salinity than that in May 1951 and *may* indicate a rather stronger northward flow. In October 1951, although the salinity at the north-end of St. George's Channel was very slightly lower than in September 1952, the salinity to the south of the Isle of Man was considerably higher; this is thought to indicate a stronger current causing greater penetration of relatively high salinity water in October 1951.

In addition to the north-going current there is also a smaller, south-going current evident near the Ulster coast at some periods. Current-meter readings at the Skulmartin Light-Vessel (Proudman, 1939) showed it to be absent or even reversed in September, October and November 1936, but present during the remainder of the 13 months investigated. Excluding the autumn months, a mean current of about 1 mile per day was shown, although in some months the average current was as much as 3 miles per day. Further current-meter readings at Skulmartin in 1953 and 1954 (Smed, 1953, 1954) have shown similar results. Unfortunately no current-meter readings are available for the periods of the present or the previous plankton surveys.

In 1951, drift-bottle returns indicated "strong *southerly* currents during the summer months of May, June and July through the Channels separating Scotland from Ireland" (Tait, 1952). Some of these bottles, released off the Mull of Kintyre, were returned from as far south as Dublin. This south-going current appears to be marked by the penetration of relatively high salinity water into the western Irish Sea (Proudman, 1946), but no salinity observations are available for this region for 1951 and 1952.

There is also some evidence of a west-going current near to the north coast of Wales. "A nearly continuous west-going stream" is recorded off the north coast of Anglesey (Admiralty, 1948), and Dr. D. J. Crisp (personal communication) considers his observations on the spread of the barnacle *Elminius modestus* to provide evidence of a west-going flow all along the North Wales coast. The most probable explanation of such a current is that it forms part of a clockwise circulation in the south-eastern Irish Sea, kept in motion by the adjoining north-going current.

THE SAMPLING METHOD AND COMPARISONS WITH THE CONTINUOUS PLANKTON RECORDER.

All samples were taken in daylight from the R.V. "William Herdman". The dates and times of sampling are given in Plates XIX and XX (upper row). The sampling instrument used was the Hardy standard plankton indicator (22 inch model with 1½ inch diameter aperture: see Hardy, 1936, and Glover, 1953). Each haul was made over 2 miles by log-line at a speed of about 7½ knots, with the indicator at a depth of approximately 17 metres. Details of the technique are given by Williamson (1952). The silk filter-discs were of 60 meshes to the inch.

The theoretical maximum volume of water filtered by a plankton indicator in a 2-mile haul is approximately 4 cu. metres, but Barnes (1951) showed that the actual volume filtered is always rather less than this. The actual volume will depend to some extent on the density and nature of the plankton.

Compared with most forms of tow-net, the plankton indicator permits the taking of many more samples at much higher speed, each sample representing a much smaller volume and a much longer and narrower column of filtered water.

In all these respects the results of the present work are more directly comparable with the results of the Hardy continuous plankton recorder surveys than with any other published plankton work.

The Hardy continuous plankton recorder as used in regular surveys of the North Sea and adjacent Atlantic waters (Rae, 1952*b*), is towed at a depth of 10 metres and sampling is continued in both darkness and daylight. The ratio of the area of the filtering surface to that of the inlet aperture is much greater in this instrument than in the standard indicator so that the theoretical maximum volume of water is probably filtered in all except very dense plankton. On this assumption the 10-mile sample, in terms of which most of the continuous recorder results are given, represents about 3 cu. metres of water. The difference between this volume and the "less than 4 cu. metres" filtered by a standard indicator in a 2-mile haul is sufficiently small to be ignored in comparing results from the two instruments, as with samples of either type only differences of $\times 3$ or more are normally regarded as significant (Barnes, 1951; Rae, 1952).

Variations due to diurnal migration of the plankton will be less marked in the indicator samples (taken only in daylight) than in the continuous recorder samples (taken in both daylight and darkness). The absence of night samples largely explains the absence of adult euphausiids from the Irish Sea samples, but the continuous recorder results suggest that the effects of vertical migration on the other groups considered are largely masked by their much greater fluctuations in horizontal distribution (Rae and Fraser, 1941; Henderson and Marshall, 1944). Except, therefore, in the case of euphausiids, the effects of differences in light intensity seem comparatively unimportant in comparing the present results with those from the continuous recorder, and the difference in sampling depths (17 metres and 10 metres) is probably also responsible for only minor differences in the samples.

CORRELATION OF THE RESULTS WITH WATER MOVEMENTS AND WATER-MASSSES.

The dispersal of any planktonic species is, by definition, principally the result of water movements. In the case of a holoplanktonic species its distribution is the result of this dispersal and its varying success in different environments, while the distribution of the planktonic larvae of benthic forms is the result of the above factors superimposed on the distribution of the parent stock. The distribution of the benthic adults is probably determined at least as much by the nature and depth of the substratum as by hydrographic conditions, and therefore any correlation of distribution with water-masses is likely to be more complex than in holoplanktonic species. The following considerations are chiefly of importance with regard to the holoplankton.

Stocks in different water-masses will, in general, encounter different environments for at least part of their history, and although it is quite possible that at any

one time a species may show similar population densities in different environments, it is to be expected that most species will not usually do so. In extreme cases these differences will amount to presence and absence. On the other hand, all differences in plankton density revealed by the present results cannot be attributed to stocks living in different water-masses. Many species have a patchy distribution even in fairly uniform physical and chemical conditions (Herdman and Scott, 1908, p. 284), and although the 2-mile hauls used in the present work tend to average out any patchiness, little hydrographic importance can be attached to any one sample of any one species. (Comments on patchiness as affecting continuous recorder results, given by Rae and Fraser (1941) p. 200, are also applicable to the plankton

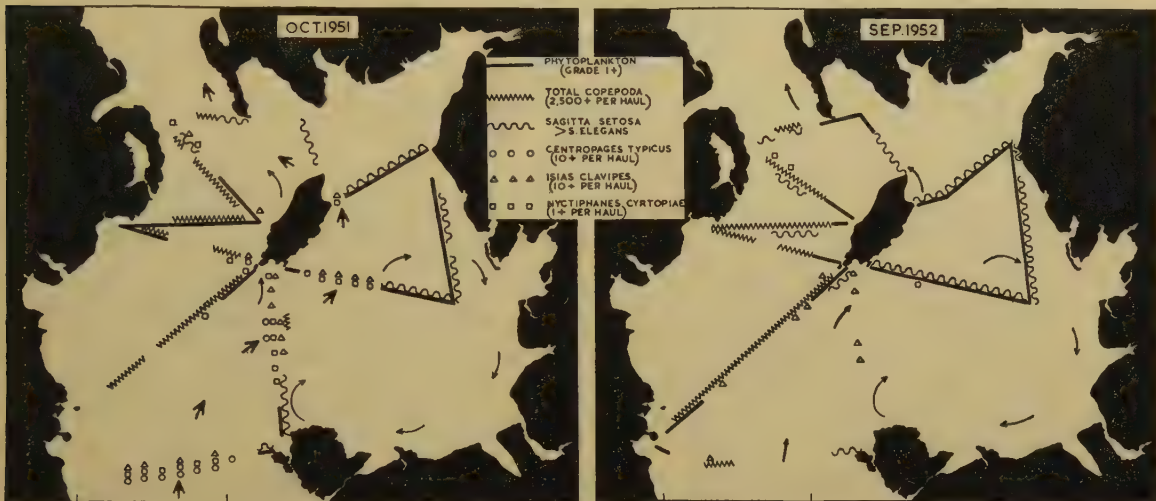


TEXT-FIG. 2.—Chart showing regions of greater density of some planktonic groups and the suggested courses of the main currents in May 1951 and May 1952.

indicator.) Also the present surveys cover up to 12 days at each period (see Plates XIX and XX) during which time many species (particularly among the phytoplankton) may show marked increases or decreases in numbers. Greater importance must therefore be attached to comparisons of population density along a single line of samples taken on the same day, than to comparisons on different lines. Tidal currents may lead to the concentration of plankton in swirls (Orton, 1937), or affect its normal vertical distribution through turbulence, and the well known fact that dense patches of phytoplankton frequently contain a much sparser zooplankton than surrounding areas must also be borne in mind in interpreting the results. However, if the average numbers of each of several species are markedly different on opposite sides of a point in a line of samples, and these differences are not attributable to the effects of tides or the inter-relationships of phyto- and zooplankton, then it is highly probable that this point lies on the boundary between two water-masses.

These principles have been applied to the results of the present surveys in the construction of Text-figs. 2 and 3. For each sampling period certain species and groups showing marked differences in quantity in different parts of the Irish Sea have been selected from the detailed results (Plates XIX–XXXI). A chart has then been constructed for each period showing those samples of each group in which the population density exceeds a certain arbitrary figure. Finally the probable currents for the period have been added to each chart as explained below.

Text-fig. 2 shows some of the main features of the distribution of total phytoplankton, total Copepoda and young stages of *Meganyctiphanes* for May, 1951 and May 1952. It has not been possible to show the individual evidence of all the



TEXT-FIG. 3.—Chart showing regions of greater density of some planktonic groups and the suggested courses of the main currents in October 1951 and September 1952.

relevant species nor to show all the relevant differences in distribution in the groups selected; both these deficiencies can only be made good by reference to the more detailed results (see following section and Plates XIX–XXXI). In spite of these limitations, however, there is abundant evidence of a band of planktonically distinct water linking St. George's Channel and the North Channel and curving in an approximate semi-circle through the eastern Irish Sea. Comparison with Plate XIX shows that samples in the band were taken under a wide variety of conditions of tidal strength and direction, and comparisons with a tidal atlas (Admiralty, 1943) shows that the band does not link parts of the Irish Sea where the maximum ebb and flow rates are attained, nor can the plankton distributions be explained in terms of swirls. The band, therefore, cannot be connected with tidal phenomena, and as it is distinguished by the scarcity of both zooplankton and phytoplankton it cannot be attributed to the inter-relationships of these groups. The only plausible explanation of the band seems to be that it marks the path of a non-tidal current,

and because of its comparative distinctness it is apparently the main current of the area. The band tends to get narrower from south to north; this suggests a north-going current in which progressive mixing with the adjoining waters on either side causes the peripheral waters of the current to lose their identity. It is also well established from physical investigations (see p. 88) that the main current of the area is north-going and tends to flow through the eastern Irish Sea, and there can be little doubt that this band shown by the plankton marks the path of this current as the arrows in the figure indicate.

The course deduced for the current in May 1951 is slightly more easterly than that in May 1952. The former course, in particular, is very similar to that derived by Bassett (1910) from temperature and salinity observations and relating to a period "when the Gulf Stream Drift is at a maximum".

The planktonic evidence for other currents in May 1951 and May 1952 is less conclusive. In May 1950 the distribution of *Calanus* gave strong evidence of a south-going current near the Irish coast (Williamson, 1952), but in May 1951, although this genus again gave some evidence of the current, it was much less striking, and in May 1952 there was little evidence of the current from this source (see p. 101 and Plate XXI). A band of relatively sparse phytoplankton is thought to indicate the course of this current in May of both 1951 and 1952 (p. 97 and Plates XIX and XX), and such a course (shown in Text-fig. 2) is in agreement with such information as is available from drift-bottles in 1951 (see p. 90).

The waters immediately north-west of Anglesey in May 1951 and May 1952 are distinguishable from those of the north-going current by their smaller numbers of copepods, particularly *Acartia* and *Oithona*, and also in May 1951 by the presence of *Phaeocystis*. The fact that this small area situated in an angle of the current maintains a distinct plankton in spite of mixing suggests that it is being constantly replenished by water with this distinct plankton. The most probable source of this replenishment is from the east, and the limited information available (Thompson, 1886; Scott, 1907; Riddell, 1913) tends to confirm the scarcity of *Acartia* and *Oithona* and the frequent presence of *Phaeocystis* off the north coast of Wales. Observations indicating the presence of a west-going current off the north coast of Anglesey are given on p. 90, where it is suggested that this current probably represents part of a large swirl in the south-eastern Irish Sea. Some confirmation of this suggestion is obtained by comparing the present results for *Sagitta* (p. 98) with those obtained by Pierce (1941). This shows that in spring the waters of the bays and estuaries may be distinguished from the remainder of the water of the south-eastern Irish Sea by the dominance of *Sagitta setosa* in the former and *S. elegans* in the latter. This is thought to represent a distinction between the circulating and non-circulating water of the area.

In October 1951 (see Text-fig. 3) the plankton shows a distinct tongue of water stretching from St. George's Channel to the north-east of the Isle of Man. It is distinguishable from the adjoining waters not only by reduced densities of phytoplankton, copepods and *Sagitta setosa* but also by increased densities of

Centropages typicus, *Isias claripes* and the late larvae of *Nyctiphanes*. This tongue, like the bands in May 1951 and May 1952, appears to mark the course of the north-going current, but now its biological character as shown on entering the Irish Sea is completely changed by the time it reaches the north of the Isle of Man. This appears to result from the current mixing with the waters of the eastern Irish Sea whose characters it largely assumes, so that beyond the north of the Isle of Man the current is marked by the dominance of *Sagitta setosa* in contrast to the dominance of *S. elegans* further south. The presence of the Isle of Man must prevent any mixing on the west side of the current for a considerable part of its course.

This current in October 1951 follows a less easterly course than in May 1951 or May 1952, and the distribution of *Nyctiphanes cyrtopieae* and of *Isias* may indicate a minor branch to the west of the Isle of Man in addition to the main flow to the east. Such a course supports the evidence from salinities and temperatures that the north-going current normally follows a more easterly course in spring than in autumn.

In September 1952 a tongue of water marked by comparatively low densities of phytoplankton and copepods and with *Sagitta elegans* more common than *S. setosa* stretched from St. George's Channel to the south of the Isle of Man, but was not distinguishable further north (Text-fig. 3). Not only did it lose its identity much more quickly than in October 1951, but it also contained very much lower densities of *Centropages typicus* and *Isias* and no *Nyctiphanes cyrtopieae*. The inference is that the north-going current was considerably weaker in September 1952 than in October 1951, and the evidence from salinities (p. 89) tends to support this view.

It will be noted that even in October 1951 when the north-going current is believed to have been relatively strong for the time of year (pp. 89 and 109–110) the planktonic character of the north-going water changed much more during its passage through the Irish Sea than in May 1951 and May 1952. This is regarded as supporting the evidence from physical observations that the north-going flow is normally weaker in autumn than in spring (see also under *Sagitta*, p. 98–99).

There is no evidence from the plankton of a south-going current in the western Irish Sea in the autumn of either 1951 or 1952. Current-meter readings (Proudman, 1939) showed that this current was stopped or reversed during September, October and November of 1936.

In October 1951 and September 1952 the relatively small numbers of *Acartia* and *Oithona* to the north-west of Anglesey again suggest an influx of water from the north coast of Wales into this region. Most of the south-eastern Irish Sea was again unsampled, and therefore the currents indicated in this area are largely hypothetical. It seems improbable that the *Sagitta* populations provide a means of distinguishing the circulating water from that of the bays and estuaries of the eastern Irish Sea in the autumn (see p. 98).

The probable currents of the Irish Sea at each period when plankton surveys were made have now been deduced from some selected features of the plankton

distribution supported by physical observations. The fact that the physical evidence frequently confirms and never conflicts with the biological evidence appears to justify both the methods used and the conclusions reached, and in the following sections the currents shown in Text-figs. 2 and 3 are assumed to have been operative at the sampling periods. The more detailed results, discussed in the following section, show to what extent these currents and the consequent separation of the Irish Sea into different water-masses affect the distribution of the individual species.

The following water-masses, which can be readily recognized in Text-figs. 2 and 3, are referred to in the text :

- (1) *the north-going current*, tending to flow to the east of the Isle of Man ;
- (2) *the south-going current* in the western Irish Sea (May samples only) ;
- (3) *central Irish Sea water* bounded on the east by the north-going current and on the west by the south-going current in May 1951 and May 1952 and by the Irish coast in October 1951 and September 1952, and
- (4) *eastern coastal water* between the north-going current and the coasts of Great Britain. This water may be subdivided into the circulating water of the south-eastern Irish Sea and the waters of the bays and estuaries, but only in the case of *Sagitta* spp. has any comparison of their plankton been found possible.

Apart from the sub-division of the " eastern coastal water " these water-masses are identical with those suggested from the preliminary surveys of 1949 and 1950 (Williamson, 1952).

DISTRIBUTION OF THE PLANKTON

Phytoplankton (Plates XIX and XX)

No detailed analysis of the phytoplankton was attempted, and only the dominant forms and approximate estimates of the density of total phytoplankton are recorded. It was found from the 1949 and 1950 surveys (Williamson, 1952) that such an analysis was sufficient to show clear correlations with the water movements of the area ; on these occasions the main concentrations occurred in regions of little residual current, while water entering the Irish Sea from the south was sparsely populated with phytoplankton.

The phytoplankton density was graded (as in the previous surveys) from the colour of the silk disc as it was removed from the plankton indicator, according to the following system :

- Grade 0 = no green-brown coloration.
- Grade 1 = green-brown coloration just visible.
- Grade 2 = green-brown coloration distinctly visible.
- Grade 3 = disc completely covered with phytoplankton.
- Grade 4 = disc very densely covered with phytoplankton.

In the case of grade 4 the filtering power of the instrument must be appreciably reduced, but it is probably little affected by the lesser densities.

Although the volume of water filtered in a 2-mile haul is similar to that filtered in a 10-mile continuous recorder sample the area of filtering silk is much greater in the case of the continuous recorder; consequently the phytoplankton grades given here do not correspond with those obtained in a similar way for the continuous recorder (e.g. Rae, 1951).

Dominant species in each area at each period are shown on the inset maps in Plates XIX and XX. In May 1952 "diatoms" refers to many species with *Chaetoceros* and *Thalassiosira* the most common.

The main concentrations of phytoplankton in May of both 1951 and 1952 were in the western Irish Sea, particularly to the west and south-west of the Isle of Man, while phytoplankton was generally sparse in the eastern half of the entrance from St. George's Channel, also between Anglesey and the Isle of Man and to the south-east of the Isle of Man. These features were also noted in 1949 and 1950 (Williamson, 1952), and the hydrographical correlations suggested from these earlier results again seem to apply. The areas of sparse phytoplankton mentioned are regarded as coming under the influence of the north-going current, while the dense phytoplankton to the west and south-west of the Isle of Man flourishes in the more stable conditions of the central Irish Sea water-mass.

The phytoplankton density showed a marked reduction near the Irish Coast in May 1951 and a smaller reduction in the same area in May 1952. These reductions, supported in May 1951 by the distribution of *Calanus finmarchicus* (p. 101), are thought to mark the path of the south-going current.

In the autumn of both years *Biddulphia sinensis* was very common in much of the eastern Irish Sea, but was almost totally absent from all other areas sampled. The distribution of this species appears to be closely correlated with that of eastern coastal water at this season. In October 1951 there was an area of sparse phytoplankton apparently coinciding with the path of the north-going current, separating the western limit of the *Biddulphia* concentration from the east coast of the Isle of Man, but in September 1952 *Biddulphia* was very common right up to the Manx coast. An explanation of this difference, confirmed by the distribution of several other species and by salinity records is that the north-going current was considerably weaker in the autumn of 1952 than 1951.

The "grade 1" phytoplankton off the Mull of Galloway in September 1952, marked "detritus" on the inset map (Plate XX) consisted of algal fragments and contained little true phytoplankton. It is thought to have resulted from local upwelling or turbulence.

Chaetognatha

Sagitta (Plates XIX and XX).

Sagitta elegans Verrill and *S. setosa* J. Müller were the only members of the genus taken during the present or the earlier surveys with the plankton indicator, but the occurrence of *S. serratodentata* Krohn in net hauls in the northern Irish Sea

in March 1950 (Fraser, 1952) is of great interest and probably indicates an unusually strong south-going current through the North Channel at that period.

The results refer only to specimens over 7 mm. in length. Smaller specimens were not normally identified to species.

The general picture of distribution in the late spring and autumn of both 1951 and 1952 appears similar to that at the corresponding periods of the previous two years. In May of both 1951 and 1952 *S. elegans* was the dominant form in all areas sampled, although *S. setosa* was probably the more common form in the bays and estuaries of the Welsh, English and Scottish coasts (*c.f.* Pierce, 1941), while at the times of the autumn samples *S. setosa* was dominant over most of the eastern and much of the northern Irish Sea. The results of the four years 1949–52 together with the results of the eight years for which Pierce (1941) analyzed samples from the Isle of Man region indicate that such a change from *elegans* to *setosa* water in most of the eastern half of the Irish Sea is a regular occurrence each autumn.

These observations may be explained on the assumption that in autumn the north-going current is either weaker than in spring or that its waters are more dilute in the constituent (or constituents) necessary for the production of *elegans* water (Wilson, 1951), or that both these factors are operating. Other evidence of a weaker north-going flow in the autumn is given on pp. 88 and 95, and this weaker flow would probably itself result in a higher proportion of coastal water in the water entering the Irish Sea from St. George's Channel. It appears that at the times of the May samples, and probably throughout the spring, *elegans* water was entering the Irish Sea from the south in sufficient quantity and of such constitution that it not only maintained its own identity throughout its passage of the Irish Sea but also exerted a dominating influence over most of the eastern Irish Sea by mixing. At this period *S. setosa* probably exceeded *S. elegans* only in the bays and estuaries where there was least penetration of this water from the south, but a minority of *S. setosa* was present in the circulating water of the south-eastern Irish Sea. Few small *Sagitta* (below 7 mm.) were taken in the south and east of the Irish Sea in the May samples. In autumn the smaller quantity or changed quality of the north-flowing water resulted in the chemical composition favouring *S. setosa* rather than *S. elegans* not only in the immediate coastal waters of the eastern Irish Sea but also in the circulating water which must contain a considerable proportion of this water from the south. Rapid and successful breeding of the relatively small numbers of *S. setosa* present in this circulating water in spring and death, or at least a cessation of breeding, of *S. elegans* is then assumed to have taken place to produce the large numbers of *S. setosa* and almost complete absence of *S. elegans* recorded in this region in October 1951 and September 1952. The presence in the eastern Irish Sea at both these sampling periods of very many *S. setosa* of between 7 and 10 mm. and of many more *Sagitta* sp. below 7 mm., some of which were recognizable as *S. setosa*, is evidence of the successful breeding of this species.

In both October 1951 and September 1952 the *Sagitta* composition of the north-flowing water changed from predominantly *elegans* to predominantly *setosa*

during its passage through the Irish Sea. This contrast with the May results for each year is again attributed to the smaller quantity and to some extent changed quality of the water entering from the south in autumn so that it is more readily changed by mixing. The fact that the current assumes the character of the waters adjoining it to the east shows that most of the mixing takes place on this side. This will probably result partly from the stronger tides on the east side, but it appears that most of the mixing takes place as the current passes to the east of the Isle of Man. Here not only is mixing with the *setosa* water to the east facilitated by strong tides and comparatively shallow water, but the island completely cuts off the current from the *elegans* water of the central Irish Sea water-mass.

In October 1951 this change in the Sagitta composition of the north-flowing water took place off the north-east of the Isle of Man and in September 1952 off the south-east. This, together with the other evidence summarized on p. 95, is regarded as indicating an appreciably weaker current in September 1952 than in October 1951.

The autumn results show *S. setosa* being carried out of the Irish Sea to the north, thus tending to confirm that specimens of this species from the Irish Sea may reach parts of the west coast of Scotland as suggested by Barnes (1950) and Fraser (1952). It seems improbable, however, that the apparently continuous distribution of *S. setosa* from the north of Ireland to the south of the outer Hebrides in August and September 1950, as recorded by Fraser, could have resulted directly from the displacement of Irish Sea water as he suggests. There is no evidence from plankton or salinities that the north-going current through the Irish Sea was unusually strong in any part of that year, and to attribute the observed distribution to outflow of Irish Sea water at the normal rate (see p. 88) would imply a steady outflow of *S. setosa* throughout the spring and summer. The fact that the species was completely absent from all samples taken in the Irish Sea in May and June (Williamson, 1952) therefore suggests that displacement from the Irish Sea could at most have been responsible for only part of the distribution off the west coast of Scotland.

The present results together with those of the 1949 and 1950 samples and many tow-net hauls taken at all seasons show the dominance of *S. elegans* in the central Irish Sea water-mass. Some consequences of this were discussed by Williamson (1952, pp. 35-39).

Polychaeta.

Small numbers of *Tomopteris helgolandica* Greef were taken at widely separated points at each sampling period. It has been recorded from all four of the main water-masses, and no pattern of distribution can be deduced from the records.

Cladocera (Plates XXI and XXII).

In addition to *Podon intermedius* Lilljeborg, *P. leuckarti* Sars and *Evadne nordmanni* Loven recorded in the earlier surveys, a few specimens of *Podon polyphemoides* Leuckart were taken off St. Bees Head in September 1952.

Jorgensen (1933) emphasized the part played by current systems on the distribution of *E. nordmanni*, stating that it occurs in every part of the North Atlantic circulation and cannot be regarded as a neritic species except in the sense that it "prefers" coastal waters as a breeding place, these being suitable for the rapid production of successive parthenogenetic broods. Regarding the Irish Sea she stated that "the main population enters via the south coast of Ireland in the current which passes through St. George's Channel and, on reaching the Irish Sea is deflected with it to the east. . . ." She assumed the species to be rare in the western Irish Sea and attributed this to the lack of influence of the north-going current on this region. The present records, particularly for May 1952, do not bear out this assumption, and they show that only small numbers of *Evadne* enter in spring with the water from St. George's Channel. However, the species reaches its greatest densities where this inflowing water mixes with the central Irish Sea water (from the south of the Isle of Man south-westward to the Irish coast) and with eastern coastal water (off the English coast and, in May 1952, to the north-east and north of the Isle of Man). The autumn samples give no evidence of recruitment from the south at this season. The fact that *Evadne* was found much further south, both off the Irish coast and south of the Isle of Man, in September 1952 than in October 1951 may be related to the weaker north-going current in September 1952, which would result in areas of comparable mixing occurring further south.

The distribution of *P. leuckarti* in spring and *P. intermedius* in autumn both show considerable resemblance to the contemporary distribution of *Evadne*, suggesting that the two *Podon* species may also have an oceanic distribution and that they can reproduce rapidly by parthenogenesis in more coastal waters. The different breeding periods of these three species might be controlled by temperature, *P. intermedius* breeding within a higher temperature range than *P. leuckarti* while the corresponding limits for *E. nordmanni* are broader and overlap with both *Podon* species.

Copepoda

The results for Copepoda include all copepodite stages, but not nauplii.

Calanus finmarchicus (Gunnerus) and *C. helgolandicus* (Claus) (Plates XXI and XXII).

The taxonomic status of these two forms of *Calanus* is undecided (Rees, 1949). They are here given specific rank more for convenience than as an expression of opinion.

Adult *Calanus* (stage VI) and Stage V copepodites were identified to the species from the shape of the last pair of thoracic appendages (Rees, 1949). Small *Calanus* (stages I-IV) of both species were grouped together and their distribution is shown separately from the large specimens.

Surveys in May and June 1950 (Williamson, 1952) showed that *C. finmarchicus* can act as an indicator of water entering the Irish Sea from the north and, in particular, of the current which frequently flows southwards along the Irish coast. Although the numbers of both species were considerably less than in the previous year, the results for May 1951 give a similar indication of this south-going current, *C. finmarchicus* being most common within 10 miles of the Irish coast. The waters round the Isle of Man and stretching west and south-west from it (central Irish Sea water) supported a predominant proportion of *C. helgolandicus*, as also did the sparsely populated waters of the north-going current, to the east of the central Irish Sea water. A few specimens of both species were taken near the English coast.

In October 1951 the dominance of *C. helgolandicus* near the Irish coast may have resulted from the absence of the south-going current (see p. 90). *C. finmarchicus* had increased considerably in the central Irish Sea water, while *C. helgolandicus* continued to enter with the north-going current, though now in larger numbers than in May. The few *Calanus* in the eastern coastal water were *C. helgolandicus*.

In May 1952 *C. finmarchicus* was even more common in the central Irish Sea water than in the previous October, and there was, in consequence, no clear distinction between this water and that of the south-going current further west. Small numbers of *C. helgolandicus* were again entering from the south, and small numbers of both species occurred near the English coast, as in the previous May.

In September 1952 *C. finmarchicus* was about as common as *C. helgolandicus* in the central Irish Sea water, and also occurred in appreciable quantities in water entering from St. George's Channel. It was, as in the previous autumn, absent from the eastern coastal water. The patch of almost pure *C. finmarchicus* near the Mull of Galloway appears to be too local to indicate an appreciable influx of water into the Irish Sea via the east side of the North Channel, but it coincides with the patch of algal detritus mentioned on p. 97, and may represent an area of local, and probably temporary, upwelling from the adjoining deep water.

It appears from the present and the earlier surveys that the *Calanus* population of the central Irish Sea water may vary considerably from time to time in the proportions of the two species present. In the waters of the north-going current, however, *C. helgolandicus* has consistently been the dominant species at all periods sampled, although *C. finmarchicus* has never been entirely absent, while in the water of the south-going current *C. finmarchicus* has generally been dominant. The population of the eastern coastal water appears from the observations available to consist of small numbers of both species in spring, but only of *C. helgolandicus* in autumn. Rees (1949) suggests that temperatures of about 15° C. and over are lethal to *C. finmarchicus*, and as this temperature is regularly exceeded in the eastern Irish Sea in the late summer it could account for the absence of this species in the autumn samples. Its re-appearance in the May samples suggests recruitment during winter and early spring from the adjoining north-going current, which probably always contains small numbers of this species.

The numbers of *C. finmarchicus* in the western Irish Sea in May 1951 and May 1952 were relatively low compared with May 1950. These numbers are likely to be affected both by the strength of the south-going current and by the density of the species to the north of Ireland one or two months previously. It appears from the summarized results published (Rae, 1951, 1952, 1953) that compared with the spring of 1950, this density was rather lower in the spring of 1951 and at least as high in the spring of 1952. The present results do not therefore clash with the opinion of Tait (1952) that the south-going current was strong in May 1951, and suggest that it was weaker in May 1952 than at the corresponding period of the previous two years.

Small *Calanus* (stage I-IV, Plates XXI and XXII) were not very abundant at any of the periods sampled, and were particularly sparse in May 1951. The greatest numbers in May of both 1951 and 1952 occurred from the Isle of Man westward to the Irish coast, and in the autumn to the west and south of the Isle of Man.

Pseudocalanus minutus Krøyer (Plates XXIII and XXIV).

Small numbers of *Paracalanus parvus* (Claus) are included in the results for this species.

Although *Pseudocalanus* was, in general, the most common copepod in the Irish Sea at each period sampled, its local abundance was often exceeded by either *Temora* or *Acartia*, and it never approached the densities recorded in May 1950, when up to 20,000 per haul were taken to the west of the Isle of Man. Although *Pseudocalanus* was rather more common in the central Irish Sea water-mass than in the north-going current at each of the sampling periods, the contrast was always much less marked than at the corresponding period of 1950.

The peridinian parasite *Ellobiopsis chattoni* Caullery occurred on specimens of *Pseudocalanus* in October 1951 and September 1952. The rate of infestation averaged about 0.3% and was fairly uniform throughout the area sampled.

Microcalanus pusillus G. O. Sars (Plates XXV and XXVI).

It is possible that when only small numbers of this species occurred in a sample they were sometimes overlooked, so that its distribution may perhaps have been rather wider than the results indicate.

Microcalanus was common to the west of the Isle of Man in May 1952, reaching 290 per haul. It also extended south and south-east of the Island as far as the edge of the north-going current. At other periods it was less common and its distribution less clearly linked with the water-masses.

Centropages typicus Krøyer (Plates XXIII and XXIV).

In 1951 and 1952, as in the previous two years, *C. typicus* was practically restricted to the autumn samples; it was not recorded in May 1951 and only once

in May 1952. In the North Sea it also occurs chiefly in autumn (Rae and Rees, 1947).

In October 1951 it was quite common at the north end of St. George's Channel, and was obviously entering the Irish Sea with the waters of the north-going current. The only occurrence of early copepodites during the present and previous surveys was in this month, but their restriction to samples between 8 and 22 miles west of Holyhead suggests that there was no appreciable breeding of the species in the Irish Sea proper at that time.

In September 1952 *C. typicus* was rare, the few specimens that were taken occurring mostly near the Ulster coast. The lack of any noticeable influx of this species from the south at this period contrasts not only with the previous year's records but also with those for 1949 and 1950, and is attributed to the weakness of the north-going current in September 1952. The few specimens near the Ulster coast present a difficulty in that there is little indication of an indigenous stock in the Irish Sea or of a south-going current at this period which could have introduced them. It may be tentatively suggested that they are the remains of an influx earlier in the year when the south-going current was flowing (*c.f.* *Nyctiphanes*, p. 107).

Centropages hamatus (Lilljeborg) (Plates XXIII and XXIV).

This species occurred in moderate numbers at each sampling period. In May 1951 it was rather more common in the waters of the north-going current than elsewhere, but this correlation was not shown at other periods. It was common off Dublin in October 1951 and September 1952.

Isias clavipes (Boeck) (Plates XXIII and XXIV)

There is a marked contrast between the results for *Isias* in May 1951, when small numbers occurred in six hauls only, and May 1952, when the species was present in half the hauls and was common both to the north and south of the Isle of Man and off Morecambe Bay. The occurrence of immature specimens in May 1952 indicates the ability of *Isias* not only to survive but also to breed in central Irish Sea water and eastern coastal water at some periods; nevertheless, the main concentrations in October 1951 and September 1952, as in the previous two autumns, were in the waters of the north-going current.

The failure of appreciable numbers of *Isias* to penetrate as far north and east in September 1952 as in October 1951 appears to be another result of the weaker north-going current in September 1952.

In the North Sea in 1938 and 1939 (Rae and Rees, 1947) *Isias* was fairly common in the late summer and autumn and showed a centre of concentration over the south-west Dogger Bank. The species appeared to be rare in water entering the North Sea.

Temora longicornis (Muller) (Plates XXV and XXVI).

In May of both 1951 and 1952 *Temora* was the most abundant copepod in many hauls in the eastern Irish Sea, although over the Irish Sea as a whole it was less common than *Pseudocalanus*. Some reduction in density in the path of the north-going current is apparent in both the spring and autumn samples.

Metridia lucens (Boeck) and *Candacia armata* (Boeck) (Plates XXV and XXVI).

In the North Sea both of these species have behaved consistently as indicators of Atlantic influx (Rae and Rees, 1947), but in the Irish Sea their occurrences have been irregular and dissimilar and have not shown any close correlation with water-masses.

Farran (1947) has recorded an instance off the south coast of Ireland in which all stages of *Metridia* completely avoided the upper 25 metres throughout the day and night, and it therefore seems possible that the species was much more common and widespread in the Irish Sea than the present results indicate. The only conclusion that can be drawn is that there is possibly a permanent resident stock in the central Irish Sea water.

Candacia was taken in only 6 samples, all in the autumn. It is possible that it, too, was more common at greater depths.

In samples taken near the south of the Isle of Man in 1909 (Herdman and Scott, 1910) the restriction of both these species to the winter months may have been an effect of turbulence associated with winter storms bringing them to the surface layers.

Anomalocera patersoni Templeton, *Labidocera wollastoni* (Lubbock) and *Parapontella brevicornis* (Lubbock) (Plates XXV and XXVI).

Anomalocera has never been common in the Irish Sea in the plankton indicator samples nor in the North Sea in the continuous recorder catches, but as the species forms surface swarms which both instruments fail to sample it is probably more common in both areas than the results indicate (Rae and Rees, 1947).

In the Irish Sea *Labidocera* was restricted to the autumn samples in 1951 and 1952, and, although slightly more common than in the previous two years, it remained a rare form. It was not restricted to any particular area or water mass. In the North Sea, on the other hand, the species was common in the summer and autumn of 1938 and 1939 when it showed a well marked centre of population (over the Dogger Bank) and its distribution closely resembled that of *Isias clavipes* (Rae and Rees, 1947.)

Parapontella was widely but rather sparsely distributed in the Irish Sea in 1951 and 1952. In the North Sea it is probably rather less common, and appears to be restricted to the south of the area.

Acartia clausi Giesbrecht (Plates XXVII and XXVIII).

As in the earlier surveys, this was the only species of *Acartia* recorded. It was rather more abundant in the autumn samples of both 1951 and 1952, but was generally very common, and was indeed the most common copepod in a number of hauls at each period sampled. It was relatively scarce near the Anglesey coast, particularly to the north of Carmel Head, at all seasons. Reasons are given on p. 90 for suggesting that this water north of Anglesey is carried westwards from the North Wales coast. The greatest concentrations of *Acartia* were always in central Irish Sea water (to the west or south-west of the Isle of Man), and it was rather less common in water entering the Irish Sea from St. George's Channel.

Continuous recorder results for the North Sea for 1938 and 1939 (Rae and Rees, 1947) indicate rather higher numbers of *Acartia* than in the Irish Sea in May and considerably lower numbers in September and October. The figures for the North Sea include small numbers of *A. longiremis* in addition to *A. clausi*.

Oithona similis Claus and *O. nana* Giesbrecht (Plates XXVII and XXVIII).

Small numbers of *O. nana* were present in a few samples in the autumn of each year, and, because of its small size, it may well have been overlooked in some other samples. As in 1950, all records were from water containing *Sagitta setosa*. *O. nana* was always rare, and the numerical results may be taken as referring to *O. similis* alone.

The greatest concentrations of *O. similis* were always in central Irish Sea water (to the west and south-west of the Isle of Man). It was scarce in the waters of the north-going current, except in September 1952, when the current was weak, and very scarce to the north of Anglesey, probably because of the drift of water from the North Wales coast into this region.

Corycaeus anglicus (Lubbock).

The only previous records of *Corycaeus anglicus* for the Irish Sea are for 1898-9 and 1910 (Moore, 1937). At both periods it was taken near Port Erin. It was also taken in Cardigan Bay (St. George's Channel) in 1905 (Scott, 1906). During the present surveys a few specimens were taken at the north end of St. George's Channel in October 1951 from 8 to 18 miles west of Holyhead. Immature specimens of *Centropages typicus* also occurred in the same samples, which appear to be in the main stream of the north-going current.

The significance of this and other unusual occurrences in the autumn of 1951 is discussed on p. 109-110.

Euphausiid Larvae (Plates XXVII and XXVIII).

As in 1949 and 1950, no adult euphausiids were taken in the plankton indicator. This is attributed to the fact that all samples were taken in daylight and comparatively near the surface (17 metres).

Meganyctiphanes norvegica (M. Sars) and *Nyctiphanes couchii* (Bell) are the only species of euphausiid recorded from the Irish Sea. Their larval stages were identified and named from the descriptions by Lebour (1924, 1925). In the present surveys *Meganyctiphanes* larvae were restricted to the May samples and *Nyctiphanes* larvae were restricted to the autumn samples, but net hauls taken round the south of the Isle of Man since 1948 have shown *Meganyctiphanes* larvae to be present throughout the spring and summer and *Nyctiphanes* larvae throughout the autumn. Both species may be taken together in this region in late August and early September (personal observations).

Comparison with the results of Frost (1932) and Glover (1952) suggests that the breeding period of *Meganyctiphanes* near the south of the Isle of Man does not differ greatly from that to either the north or the south of Ireland, but that that of *Nyctiphanes* is much more restricted than in either of these latter areas. To the north of Ireland *Nyctiphanes* breeds at least from April to November and to the south of Ireland from February or March to November. While it is possible that breeding may begin earlier in some parts of the Irish Sea than near the south of the Isle of Man, the absence of *Nyctiphanes* larvae from the May samples for 1949, 1950, 1951 and 1952 shows that all breeding in the Irish Sea must begin much later than to the north and south of Ireland.

In May of 1951 and 1952 eggs and larvae of *Meganyctiphanes* were taken in greatest numbers round the south of the Isle of Man and westwards and north-westwards from the Island to the Irish coast. Smaller numbers occurred in the southern Irish Sea and the north end of St. George's Channel, and only very occasional specimens were obtained from the eastern Irish Sea. Adult *Meganyctiphanes* are known to occur in the deeper water to the west of the Isle of Man (Moore, 1937, and unpublished records of the Marine Biological Station, Port Erin), and local breeding is thought to account for most of the larvae recorded in the present work. The sparseness of larvae in the waters of the north-going current suggests either that adults are sparse in St. George's Channel or that their breeding period differs considerably from those in the Irish Sea. It seems possible that some *Meganyctiphanes* larvae, spawned to the south of Ireland at the peak period of April and May (Frost, 1932), may reach the Irish Sea in the waters of the north going current in the late summer or autumn, but none were recorded in the present surveys. *Meganyctiphanes* larvae south of Ireland are only about one third as common as those of *Nyctiphanes*; these latter are thought sometimes to reach the Irish Sea in moderate numbers from this area (see below).

The scarcity of records of adult *Nyctiphanes* from near the south of the Isle of Man suggests that it is present in small numbers only, but as it is most likely to occur in night samples (Frost, 1932; Glover, 1952) and few of these have been taken in other parts of the Irish Sea in recent years, little is known of its occurrence in these other areas. As the species is believed to have increased its range considerably during the present century (Einarsson, 1945; Marshall, 1948) lack of mention in earlier records may not reflect the present position.

Unlike *Meganyctiphanes*, the eggs of this species are not shed into the water (Lebour, 1924). In October 1951 and September 1952 larvae of *Nyctiphanes* were widely dispersed in moderate numbers in the waters of the north-going current and the central Irish Sea, but were not taken in eastern coastal water. In October 1951 the later stages (cyrtopiae) were practically restricted to the waters of the north-going current, in which they were fairly common. In September 1952, however, very few cyrtopiae were taken, and no distinction could be made between the north-going current and the central Irish Sea water on the basis of their *Nyctiphanes* populations. Although the samples for September 1952 were taken about 3 weeks earlier in the year than those for October 1951, this difference in dates does not explain the difference in the results, for cyrtopiae were present to the west and north of Anglesey and south of the Isle of Man in early September 1950 about two weeks earlier in the year than the 1952 samples. From observations by Frost (1932) on the occurrence of the different stages of *Nyctiphanes* south of Ireland and from statements by Einarsson (1945) on the rate of development of some other euphausiids, it seems probable that a cyrtopia larva of *Nyctiphanes* must be at least $2\frac{1}{2}$ months old. Local breeding of the species near the south of the Isle of Man does not appear to take place before late August, and then only on a small scale, so it appears that all cyrtopia stages occurring in this region before early November must have come from other breeding grounds. It seems possible that breeding of the species in the southern Irish Sea and St. George's Channel may commence earlier than near the Isle of Man, and that these former areas may be the source of some of the cyrtopiae taken in the Irish Sea in September and October. A more probable source of the bulk of these larvae, however, is in the waters to the south of Ireland, where *Nyctiphanes* is known to be abundant, with a breeding peak from April to June (Frost, 1932). That larvae from this brood should occur in the southern half of the Irish Sea in the late summer and autumn would be in agreement with Proudman's (1948) estimate of about 1 mile per day for the average flow of the north-going current. If this theory correctly explains the origin of the cyrtopiae associated with the north-going current in October 1951, the lack of such an association in September 1952 must be attributed either to a comparative failure of the spawning of *Nyctiphanes* to the south of Ireland in 1952 or to a comparatively much weaker north-going current during the autumn of that year. There is considerable confirmatory evidence for this latter suggestion (see p. 95).

In both October 1951 and September 1952 a very few cyrtopia larvae were taken in the north-western Irish Sea. (Three specimens were taken at each of these periods.) Their presence can not be connected with the north-going current, and it is suggested either that they may signify an earlier commencement of breeding in this area than near the south of the Isle of Man or that they mark the remains of an influx through the North Channel earlier in the year when there was a south-going current (*c.f.* *Centropages typicus* p. 103). No influx of *Nyctiphanes* larvae with the south-going current was noted in May of either year, but at this period the spawning to the north of Ireland was probably only just reaching its peak (Glover,

1952), and the larvae hatched then would probably not reach the Irish Sea for about another two months. (The rate of flow of the south-going current is discussed on p. 90.)

Decapod larvae (Plates XXIX and XXX).

I am greatly indebted to Dr. C. B. Rees for many useful hints on the identification of larval decapods, and for placing at my disposal keys and references to literature which he had compiled.

Results for decapod larvae are given in rather less detail than for most of the zooplankton. Plates XXIX and XXX give the total number of larvae per sample and the species in each group of (usually) 3 samples. The following taxonomic notes refer to the list of species given with the plates.

Hippolyte spp. includes both *H. varians* Leach and *H. prideauxiana* Leach, but the two species were not distinguished in the majority of hauls.

Galathea squamifera Leach: the figure of a stage I larva of *G. squamifera* given by Lebour (1931) shows the lateral spines on the 4th abdominal segment as being much shorter than those on the 5th, and this character was used by Bull (1936) in his key to the larvae of the genus. In the majority of the Irish Sea specimens, however, both from laboratory hatchings and from the plankton, the spines on the 4th and 5th segments were of equal length (similar to those illustrated by Lebour on the 5th segment) and only in the smallest specimens were the spines on the 4th segment noticeably the shorter.

Callianassa sp.: Rees (1952) gives good reasons for believing the larva described by Webb (1921) and Gurney (1942) under the name *C. subterranea* (Montagu) to belong to *C. tyrrhena* (Petagna) (= *C. laticauda* Otto = *C. stebbingi* Borradaile)¹. Larvae agreeing with these descriptions were taken in October 1951 and September 1952. There are only 2 records of adult *Callianassa* from the Isle of Man area, each consisting of a single chela. Both have been identified as *C. tyrrhena*.

Anapagurus spp. includes *A. hyndmanni* (Thompson), *A. laevis* (Thompson) and *A. chiroacanthus* (Lilljeborg), but the first stage larvae could not be separated with any certainty in the preserved material.

Portunus spp. and *Inachus* spp.: the species could not be distinguished in the preserved material (Lebour, 1928).

Pirimella denticulata (Montagu)?: these agree with the larvae described by Lebour (1928) as probably belonging to this species.

In the May samples *Corystes cassivelaunus* attained numbers far exceeding those of any other species. One haul off St. Bees Head in May 1951 included 284 specimens, while in May 1952 the greatest numbers (140 per haul) occurred some 20 miles further south. There was no species of comparable abundance in the autumn samples.

Nearly all species were more common in the shallower regions sampled,

¹ Further observations on the identity of these larvae are made by Rees (1955): Bull. mar. Ecol., IV, 29, p. 73.

particularly in the eastern Irish Sea. The deeper parts of the western (and particularly the south-western) Irish Sea yielded few decapod larvae at any of the sampling periods. Tow-net hauls to the west of the Isle of Man suggest that larvae of *Nephrops norvegicus* are normally more common in daylight at greater depths than those of the present samples (17 metres), and it is possible that the vertical distribution of other species may have produced a misleading picture of their abundance in the results. It seems probable, however, that those decapods whose larvae were common at 17 metres at the times of the plankton surveys are themselves uncommon in areas deeper than about 60 metres (33 fathoms) in the Irish Sea.

With one exception, adults corresponding to all the larvae taken have been recorded from the Irish Sea. The exception is *Spirontocaris gaimardi*, whose larva was taken only once, to the west of Anglesey in September 1952. Apart from those larvae of which there were only one or two records, none was restricted to any one water-mass, and our incomplete knowledge of the distribution of the adults in much of the Irish Sea and in the adjoining areas to north and south makes it impossible to relate the distribution of the larvae to water movements with any certainty.

Appendicularia (Plate XXXI).

Members of this group were frequently considerably damaged in the plankton indicator, and complete identification was often impossible. It is thought, however, that the vast majority of specimens were *Oikopleura dioica* Fol except to the south-east of the Isle of Man in May 1951 when *Fritillaria borealis* Lohmann was fairly common.

Oikopleura showed a patchy distribution not obviously related to hydrographic features. It was unusually rare in May 1951 in all areas except the south-west.

Other species.

Although not taken in the plankton indicator, the occurrence of two species in the Isle of Man area in the autumn of 1951 is sufficiently unusual to be worthy of note. About a dozen specimens of *Veleva spirans* (Forskal) were washed up on the north-east of the Isle of Man on September 7, and single specimens of the larva of *Squilla desmeresti* Risso were taken in tow-nets off the south-east of the Island several times in October and early November. All the *Squilla* larvae were in 7th pelagic stage, and neither adults nor young larvae have been recorded from the Irish Sea. *Squilla* larvae have several times been taken from parts of St. George's Channel in the late summer (Scott, 1906 and 1907), but here again the records are of later stages only and it is possible that they were hatched considerably further south. Adult *Squilla desmeresti* have frequently been taken in the western English Channel (Marine Biological Association, 1931) and it is probable that they also occur to the south of Ireland.

In addition to these two unusual occurrences the results for October 1951

indicate that the range of *Corycaeus anglicus* (p. 105) and the breeding range of *Centropages typicus* (p. 103) extended unusually far north in St. George's Channel and the Irish Sea. All these records are consistent with a north-going current of greater than average strength at this time.

DISCUSSION.

One of the most remarkable features of Irish Sea plankton is the number of species which fail to occur. Currents enter the area from the Atlantic through both St. George's Channel and the North Channel, and yet the vast majority of those thaliaceans, euphausiids, copepods, pteropods, chaetognaths, and siphonophores which have been associated with Atlantic penetration in other European waters have seldom, if ever, been recorded from the Irish Sea (*c.f.* Russell, 1935, 1939; Rae and Rees, 1947; Marshall, 1948; Fraser, 1952; Glover, 1952).

It might be suggested that these absences are only apparent and result from inadequate sampling. While, however, the present work was restricted to the late spring and autumn and much of the earlier plankton work in the Irish Sea was concentrated round the south of the Isle of Man (*e.g.* Herdman and Scott, 1908–1921), there are several investigations including Scott (1906, 1907) and Riddell (1913, 1914) and the combined records from numerous isolated hauls included by Moore (1937) to which these restrictions of place and season do not apply. It can only be concluded, therefore, that the volume of Atlantic water transported to the Irish Sea is too small and its rate of flow too slow for the majority of Atlantic indicator species to reach the Irish Sea. What is known of the rate of flow of the two currents (pp. 88 and 90) supports this view, for it appears that a planktonic organism would take, on average, about three months to pass through St. George's Channel and about two months to pass through the North Channel into the Irish Sea.

Of those species which have been regarded as indicators of Atlantic influence in the English Channel and North Sea only *Nyctiphanes couchii* and *Centropages typicus* appear to behave as indicators of the influx of water into the Irish Sea in normal years, while *Sagitta serratodentata* (p. 97) and *Limacina retroversa* (Moore, 1937) may occasionally reach the area under exceptional conditions. On the other hand, several species which behave as indicators of some admixture of Atlantic water in the North Sea and English Channel appear to be resident in the Irish Sea; in this category are *Meganctiphanes norvegica*, *Sagitta elegans* and *Metridia lucens*. The central Irish Sea water-mass seems to provide sufficiently deep water and sufficiently stable conditions for these species (Williamson, 1952).

In the present work *Isias clavipes* and *Corycaeus anglicus* have also been regarded as indicators of water entering the Irish Sea from the south in the autumn. These are not Atlantic species, but are presumed to be normally resident near the southern end of St. George's Channel. No adequate explanation can be offered as to why they are not permanent residents of the Irish Sea.

It may appear paradoxical that while several species can act as planktonic

indicators of water entering the Irish Sea from the south in September and October (pp. 94-5 and 109) none appears to do so in May, and yet it is suggested (p. 95) that the flow from the south is normally stronger in spring than in autumn. The explanation lies in the time taken for water to pass through St. George's Channel and in the seasonal fluctuations in abundance shown by most species. Thus for a species to act as a "southern" indicator in the Irish Sea it would have to have been abundant near the southern end of St. George's Channel or to the south of Ireland some three or four months previously. The observations in the Irish Sea, therefore, suggest that several species which are uncommon as residents of the Irish Sea are frequently abundant in these more southern localities in the late spring and early summer, but that no such species is normally abundant here in the winter.

Both physical and biological oceanography would benefit from a direct measurement of the rate of flow of the north-going current (*c.f.* Bowden, 1950), and it now seems possible that such a measurement could be made from observations on the progress through St. George's Channel of those forms which can behave as "southern" indicators in the Irish Sea in the autumn (*e.g.* *Nyctiphanes* larvae and *Centropages typicus*). The plankton also provides the means of comparing the rate of the north-going current in the autumn of different years by the relative rate of change of the planktonic character of the water as it flows through the Irish Sea. This is shown by both the distance of northward penetration of "southern" indicators and by the position of the western boundary of *Sagitta setosa* and *Biddulphia sinensis*. The lack of "southern" indicators in the Irish Sea in May seems to prevent any planktonic measurement of the absolute rate of flow of the current during the early part of the year. In May, also, the planktonic character of the north-flowing water does not appear to change appreciably in the Irish Sea, and the only planktonic indications of the course of the current consist of variations in the density of ubiquitous species. Under these circumstances, unless the course itself can be linked with the rate of flow, there seems no means of deducing from the plankton whether the current is above or below average strength.

If the suggestion (p. 107) is confirmed that *Nyctiphanes* larvae from the waters to the north of Ireland can enter the north-western Irish Sea in the summer, then observations on the rate of progress of these larvae through the North Channel might be used to measure the rate of flow of the south-going current during the late spring and summer, and the density and distance of southward penetration of the larvae at any given period might give indications of the relative rate of flow. Similar observations on *Calanus finmarchicus* might be used in the same manner, but greater difficulty would probably be experienced in some years in distinguishing the invading and indigenous stocks of this species.

SUMMARY.

Plankton surveys covering most of the Irish Sea were made in May and October 1951 and May and September 1952. The sampling instrument was the standard

Hardy plankton indicator, and samples were analysed for phytoplankton, non-larval zooplankton (except medusae), and euphausiid and decapod larvae.

From some features of the plankton distribution at each of the periods when samples were taken, a north-going current, passing to the east of the Isle of Man, can be deduced. There is also evidence of a clockwise swirl in the south-eastern Irish Sea, and, at the times of the May samples, of a south-going current near the Irish coast. Evidence of these water-movements is shown independently by many species and agrees closely with that from physical sources.

Comparisons are made between Irish Sea plankton and that of the North Sea and English Channel regarding resident species and "indicators" of in-flowing water.

Some hydrographic features which might be deduced from Irish Sea plankton are discussed.

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EXPLANATION OF PLATES.

PLATES XIX AND XX.

The upper row of charts show the routes over which samples were taken with the Plankton Indicator during four cruises in May 1951, May 1952, October 1951 and September 1952. The time (G.M.T. + 1 hr.) and the date are given at the beginning and end of each line of stations and the arrows indicate the strength and direction of the tidal stream at the time of sampling. Contemporary surface salinity observations are also shown.

The middle row of charts show "total phytoplankton" per sample during May 1951, May 1952, October 1951 and September 1952 graded according to an arbitrary colour scale. The inserts give the distributions of the dominant species.

The lower row of charts show the distribution of *Sagitta elegans* (black circles) and *Sagitta setosa* (open circles) during May 1951, May 1952, October 1951 and September 1952. The key refers to the numbers caught per 2-mile haul or approximately per 4 cu. metres of water filtered.

PLATES XXI AND XXII.

Charts showing the distributions of four species of *Cladocera* (upper row), late stages of *Calanus* (middle row) and young stages of *Calanus* (lower row), in May 1951, May 1952, October 1951 and September 1952. The keys refer to the numbers caught per 2-mile haul or approximately per 4 cu. metres of water filtered.

PLATES XXIII AND XXIV.

Charts showing the distribution of *Pseudocalanus* (upper row) *Centropages* spp. (middle row) and *Isias* (lower row) in May 1951, May 1952, October 1951 and September 1952. The keys refer to the numbers caught per 2-mile haul or approximately per 4 cu. metres of water filtered.

PLATES XXV AND XXVI.

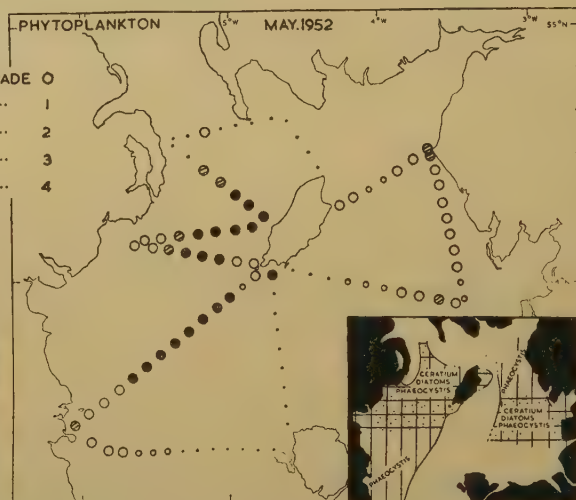
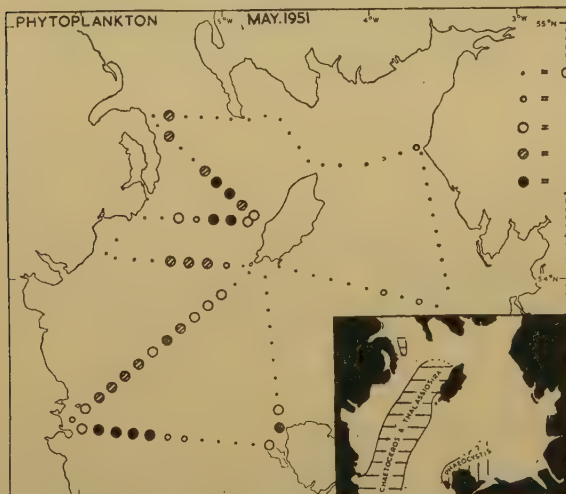
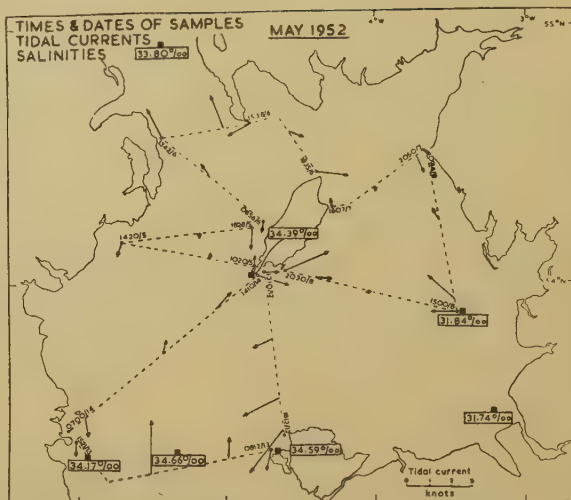
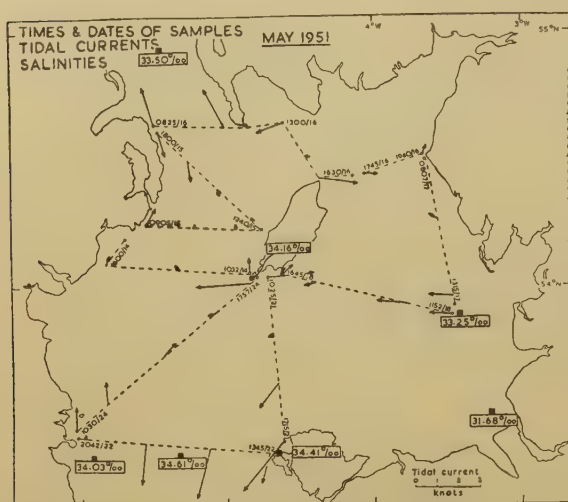
Charts showing the distribution of *Temora* (upper row), *Metridia* and *Candacia* (middle row) and *Microcalanus*, *Anomalocera*, *Labidocera* and *Parapontella* (lower row) in May 1951, May 1952, October 1951 and September 1952. The keys refer to the numbers caught per 2-mile haul or approximately per 4 cu. metres of water filtered.

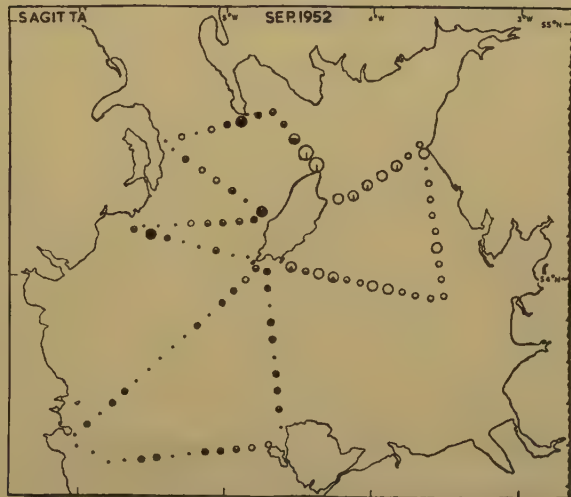
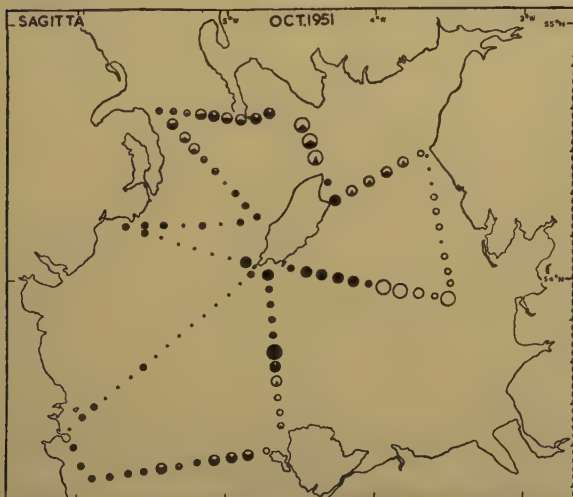
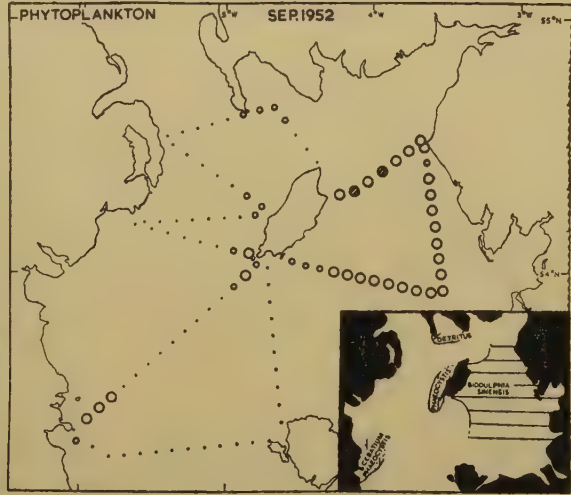
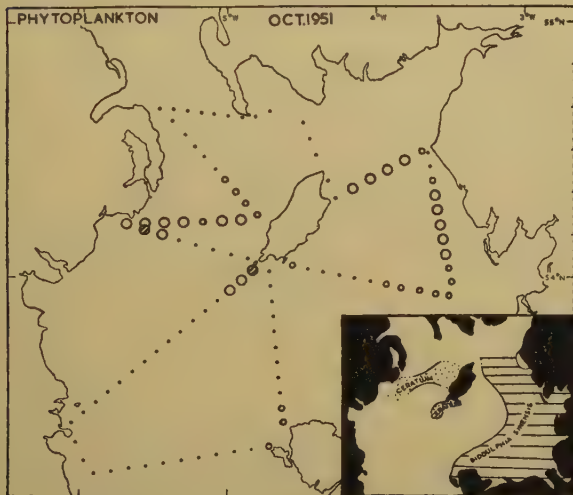
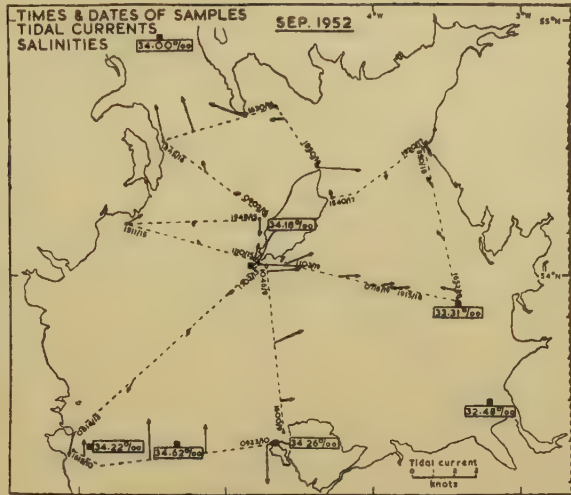
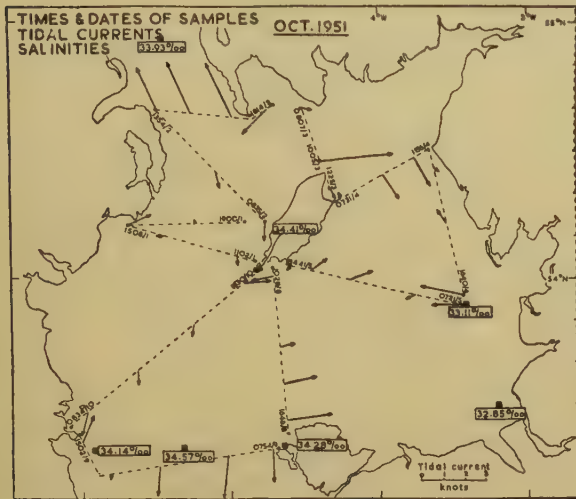
PLATES XXVII AND XXVIII.

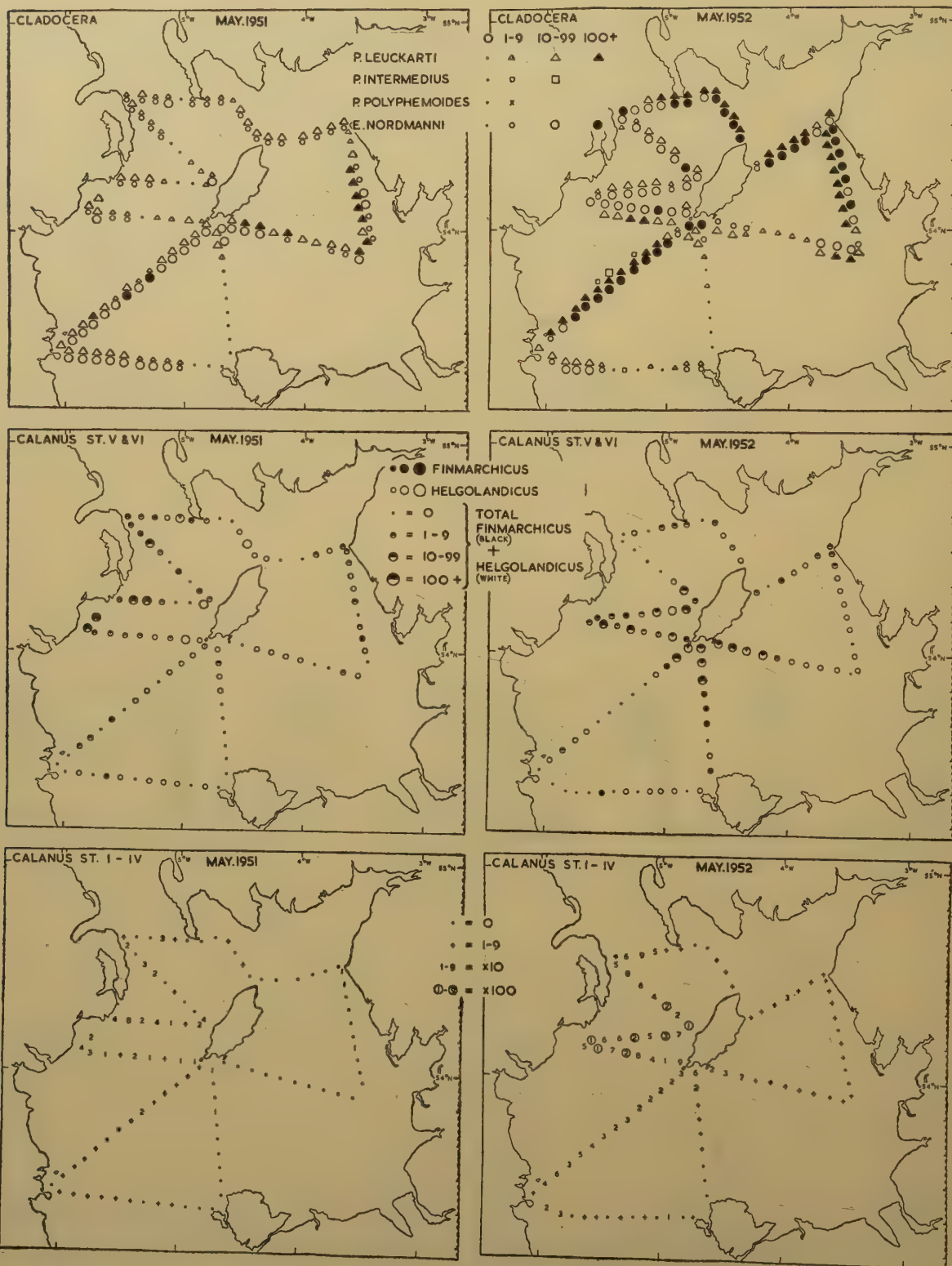
Charts showing the distribution of *Acartia* (upper row), *Oithona* (middle row) and euphausiid larvae (lower row) in May 1951, May 1952, October 1951 and September 1952. The keys refer to the numbers caught per 2-mile haul or approximately per 4 cu. metres of water filtered.

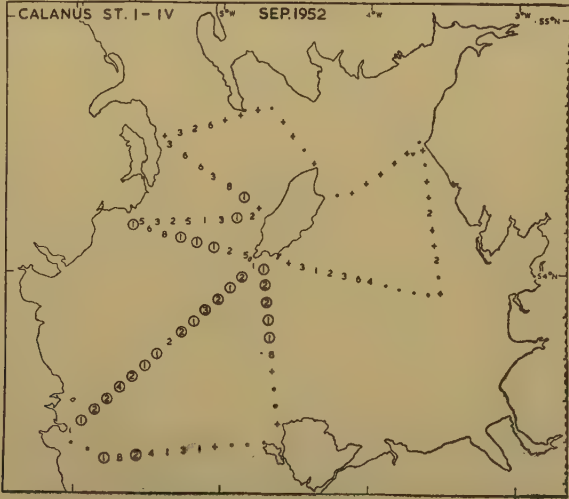
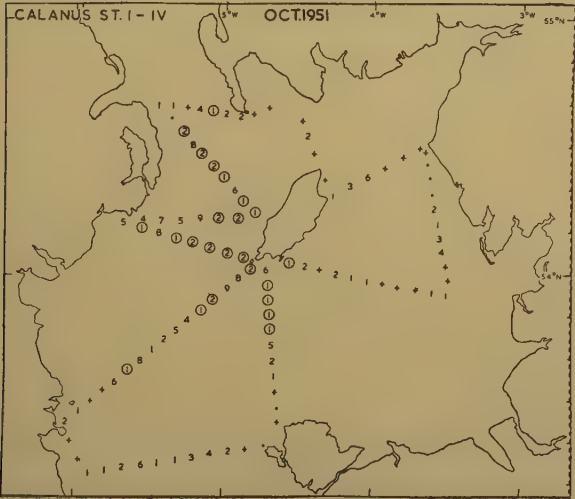
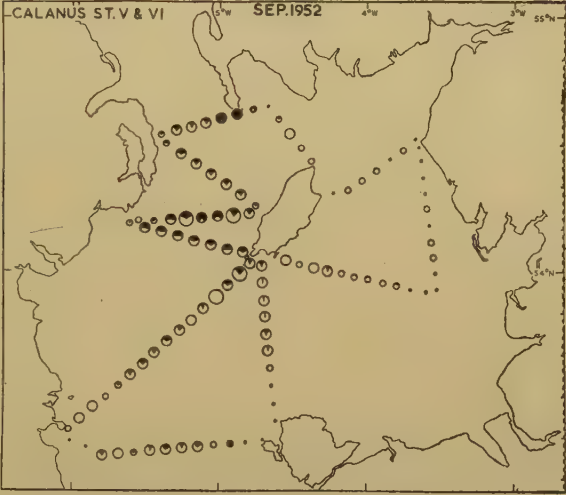
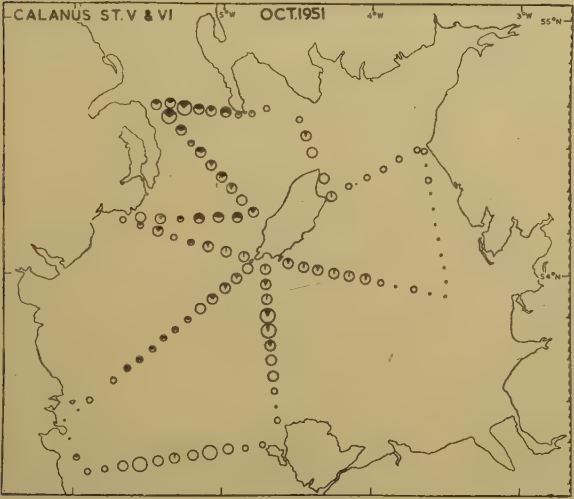
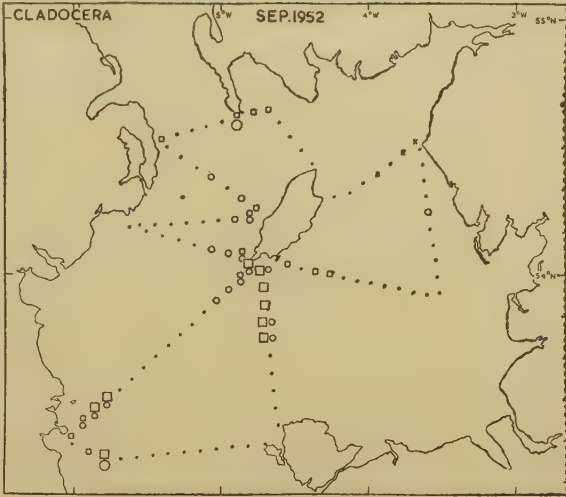
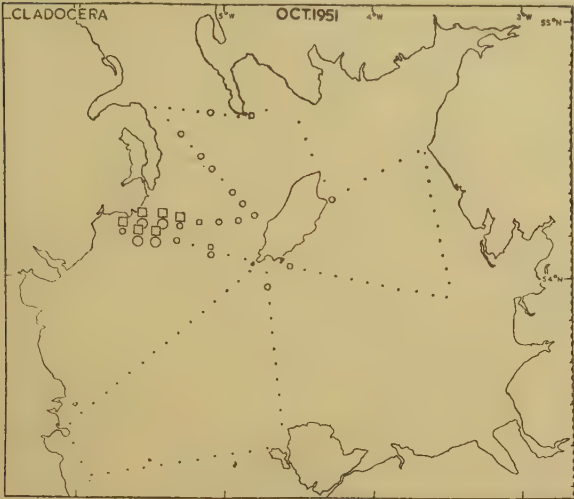
PLATES XXIX, XXX, AND XXXI.

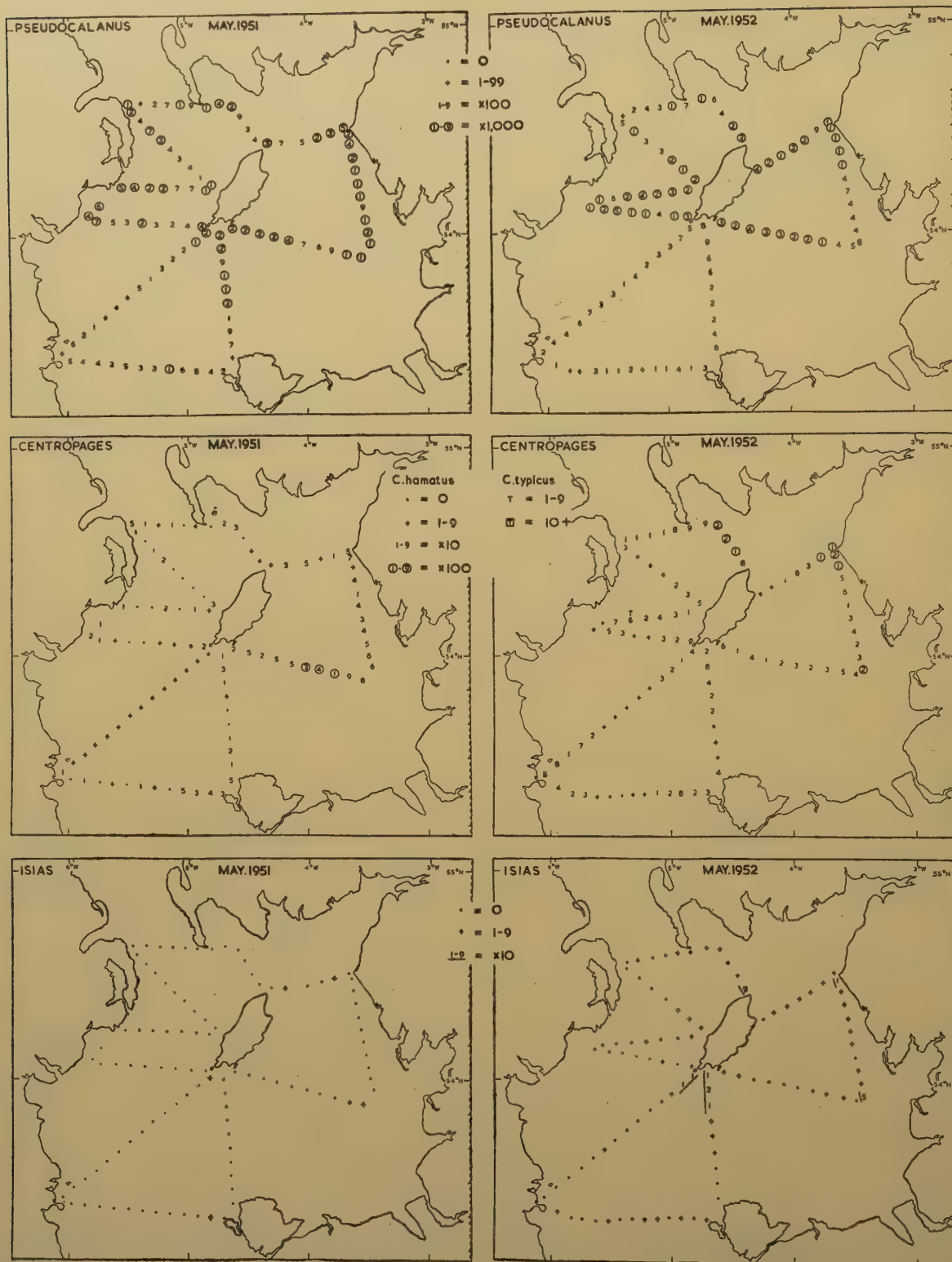
Charts showing the distribution of decapid larvae and Appendicularia; further explanation on plates.

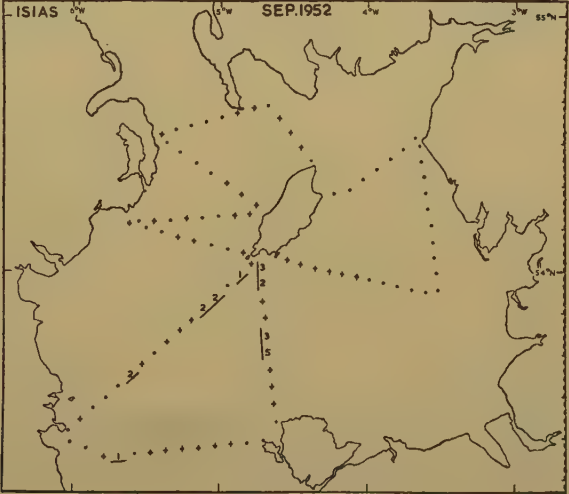
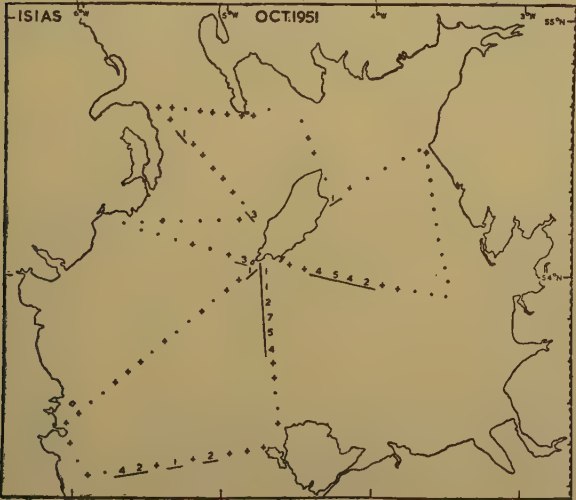
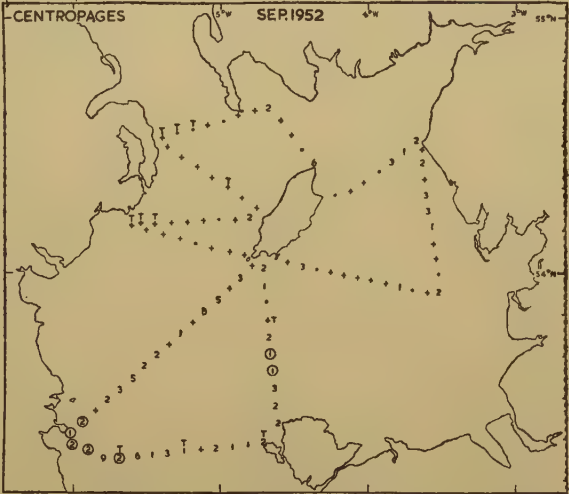
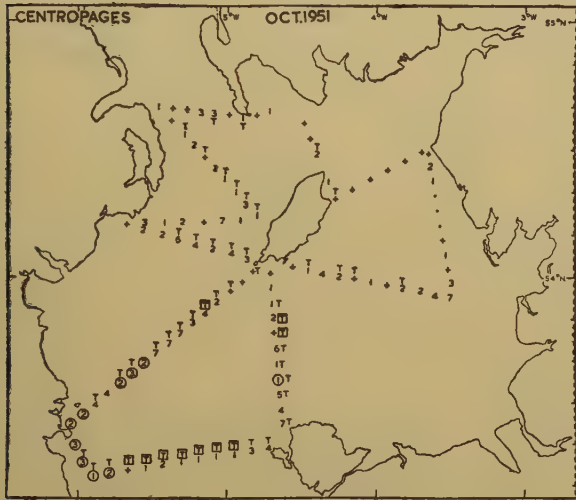
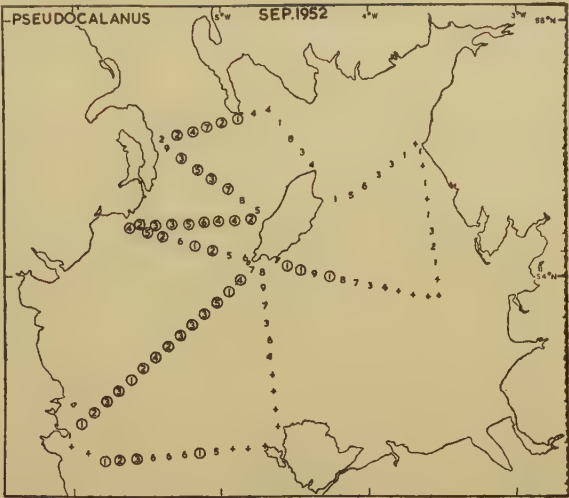
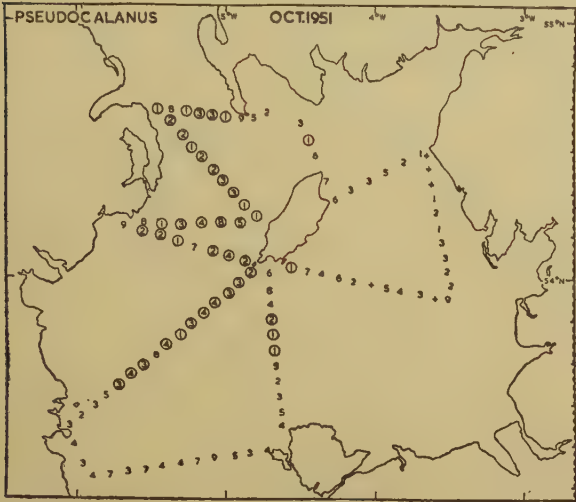


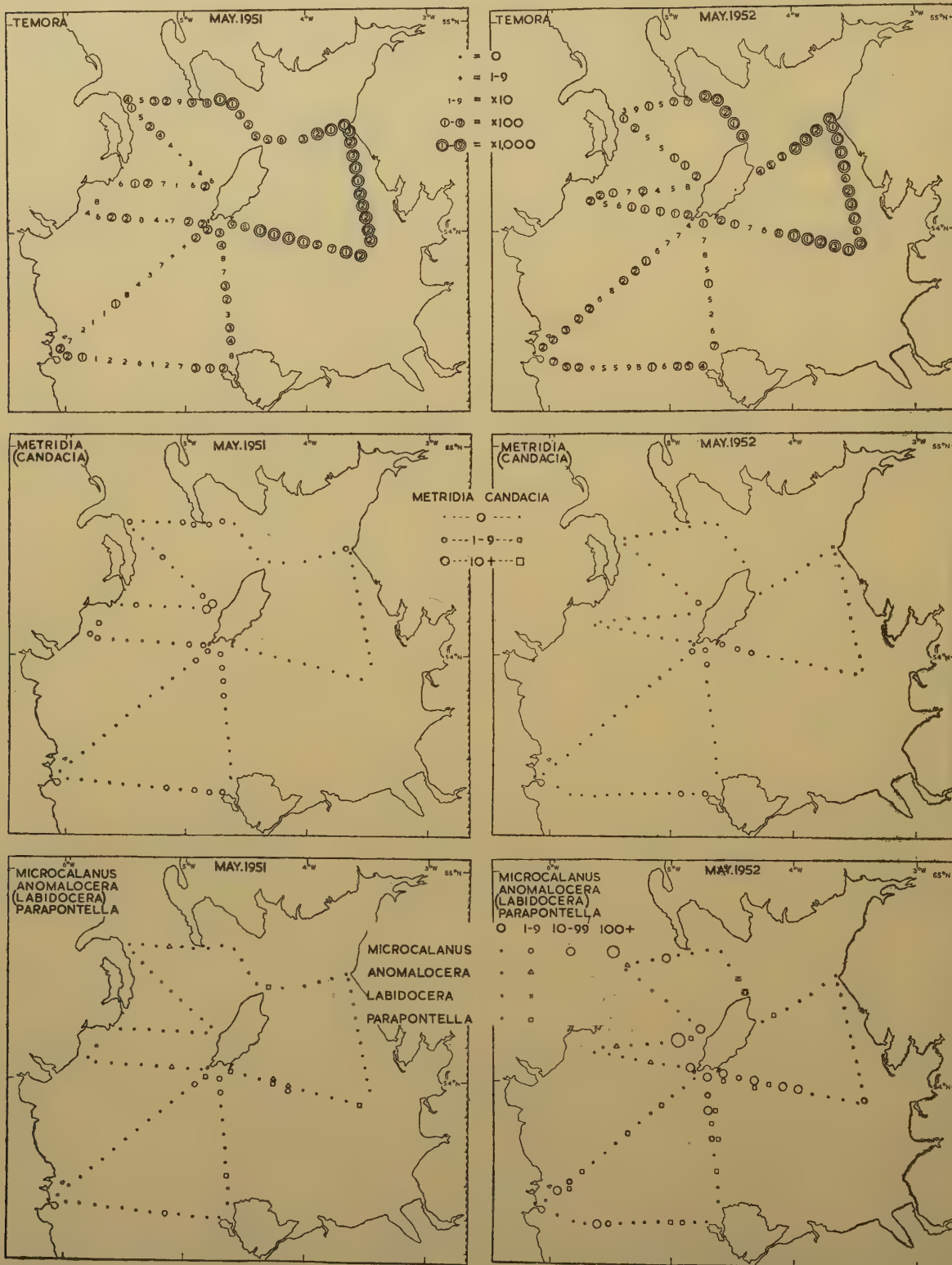


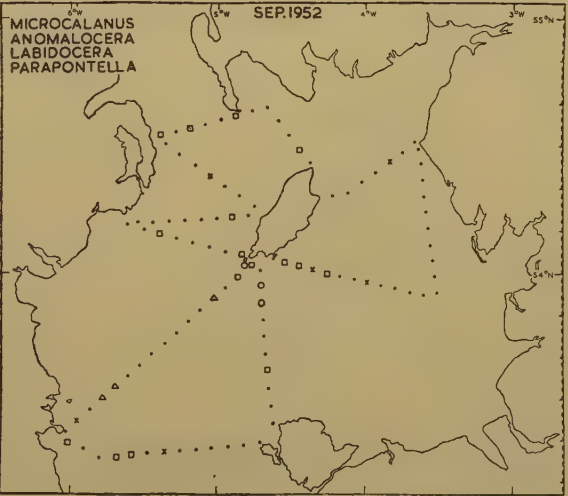
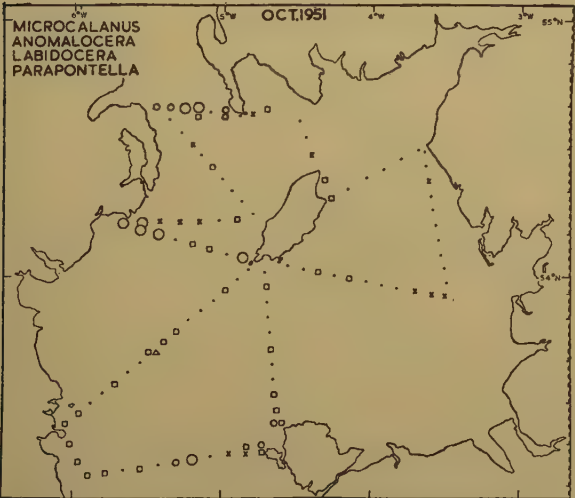
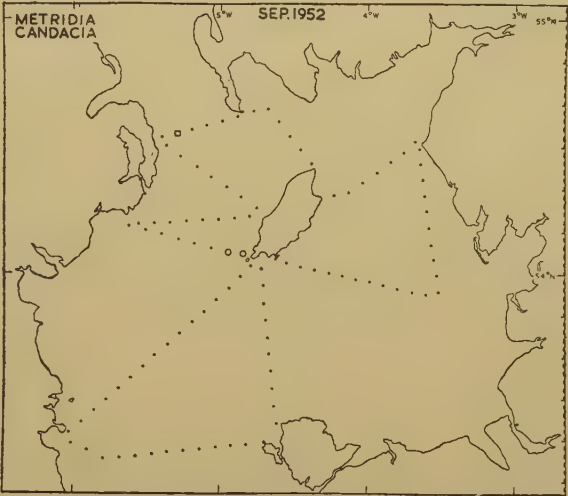
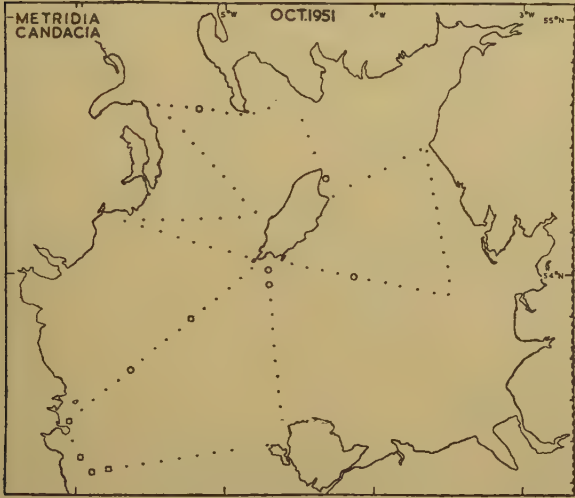
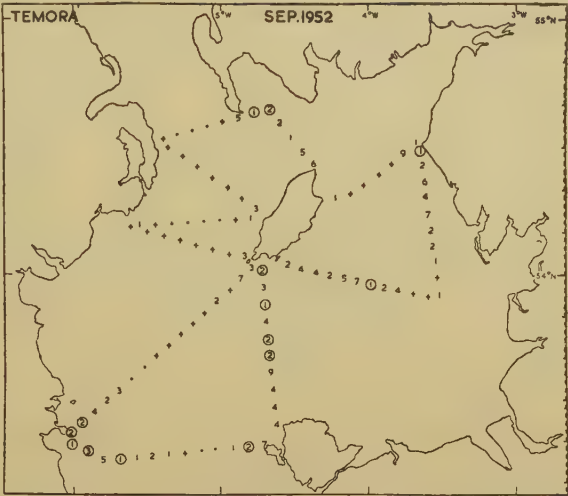
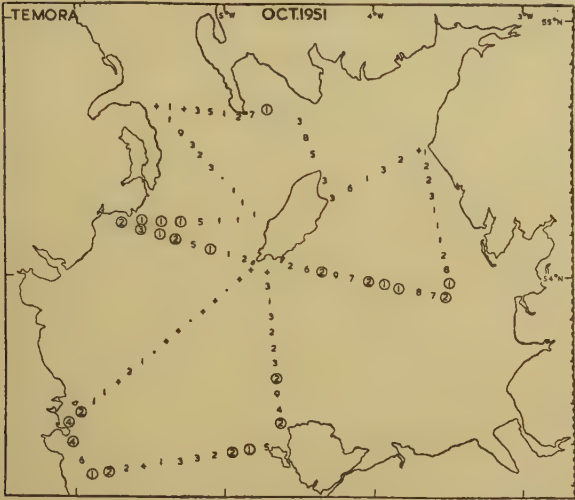


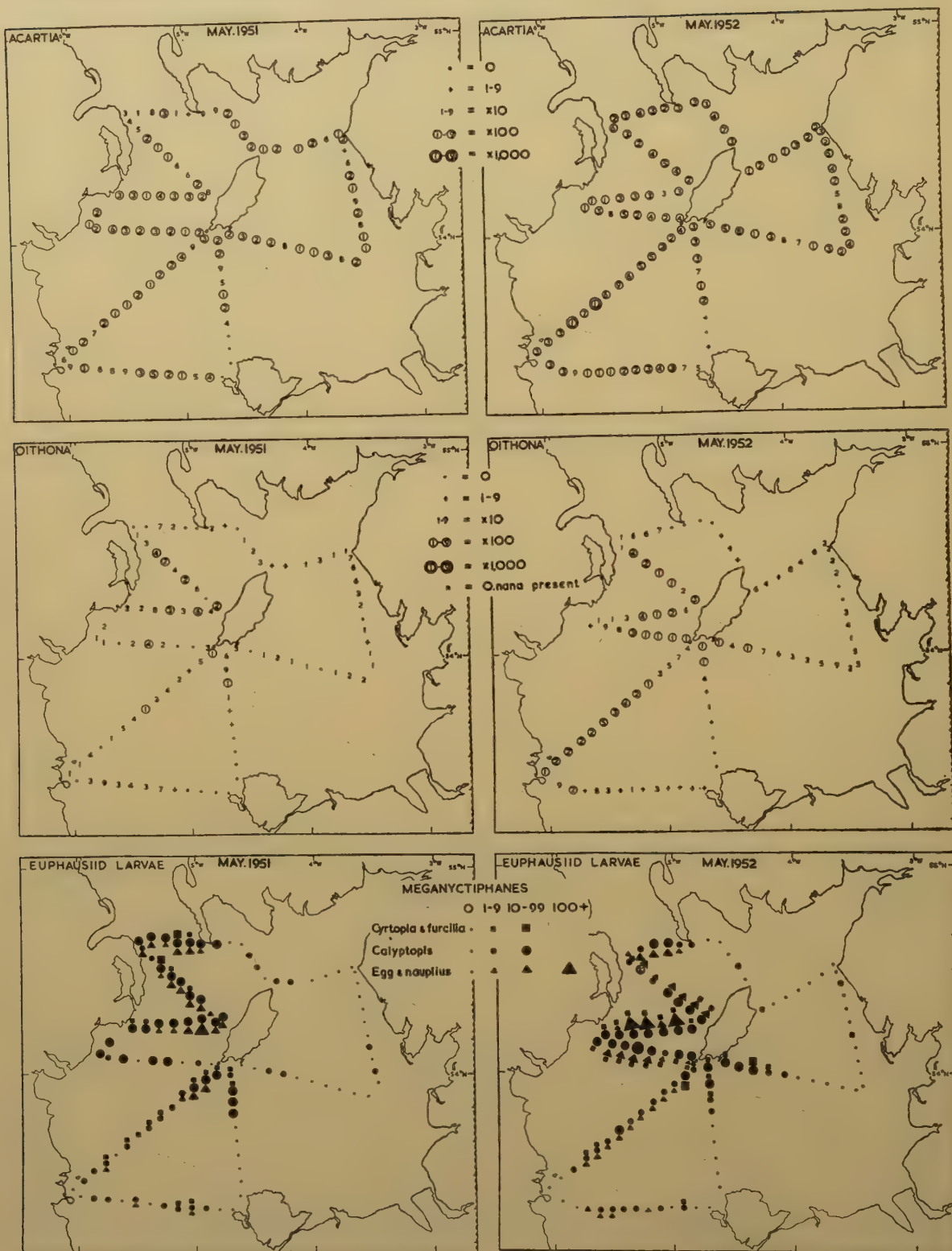


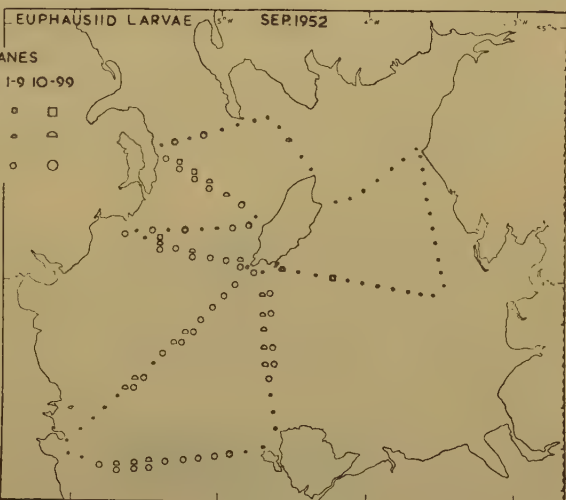
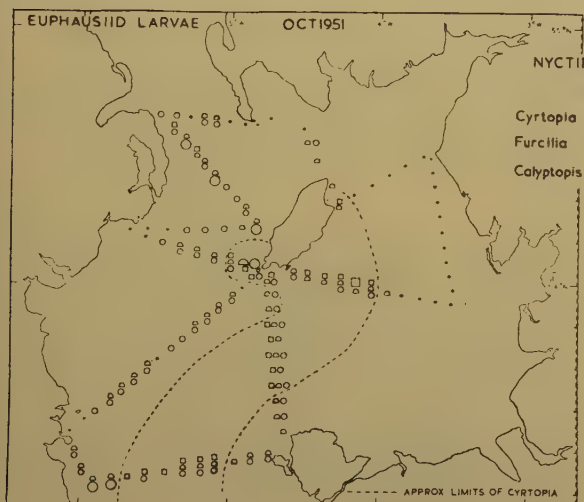
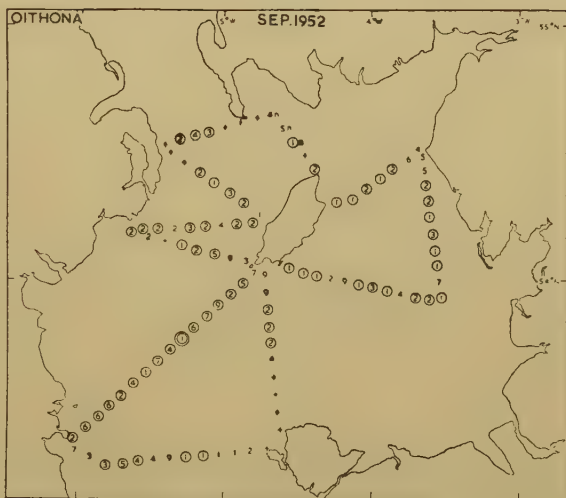
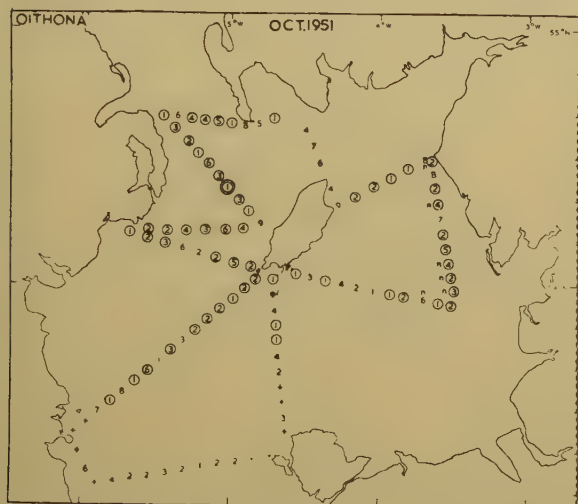
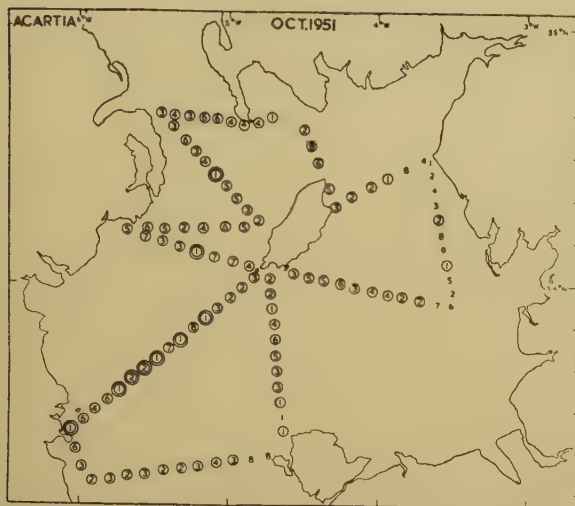






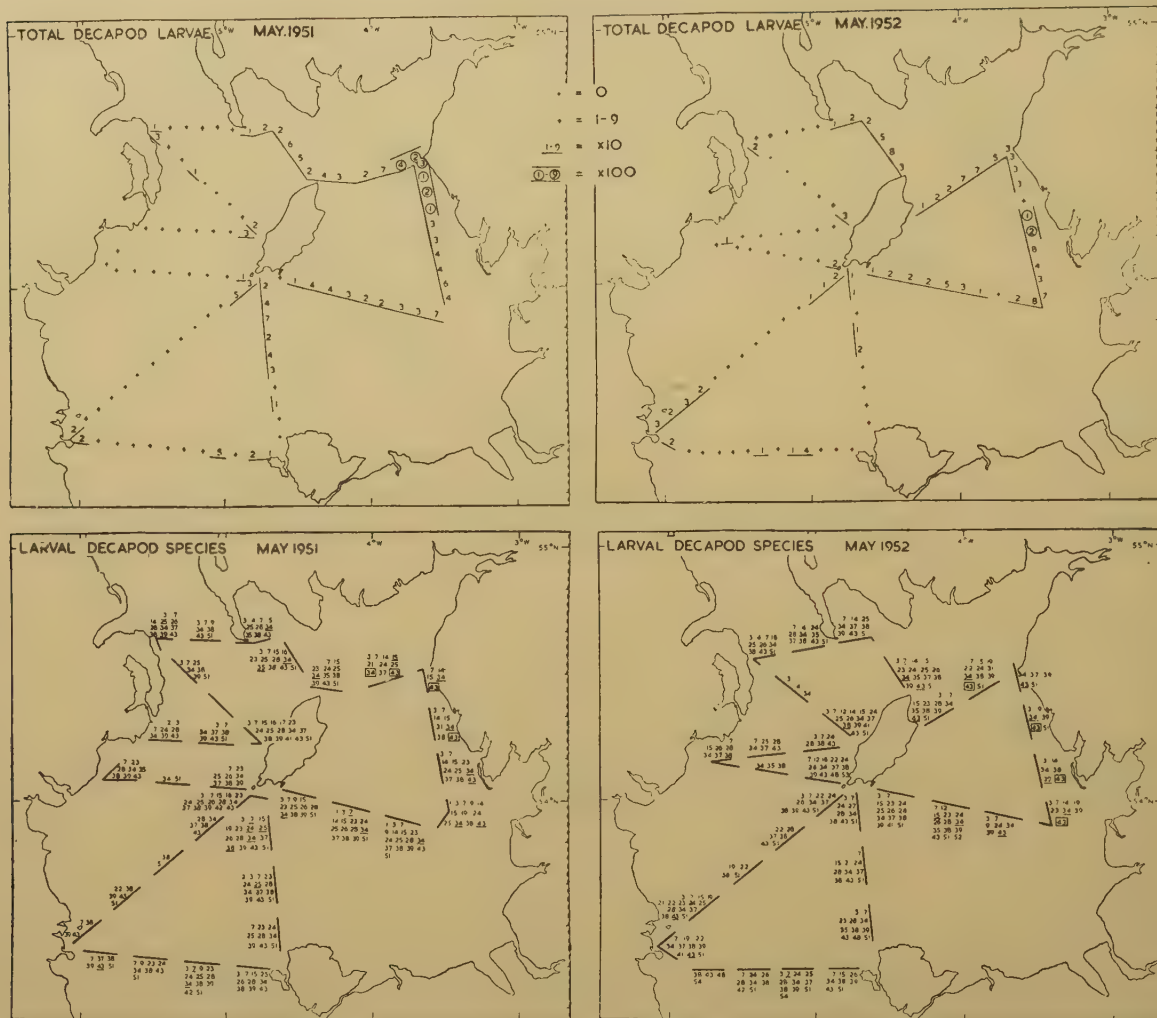






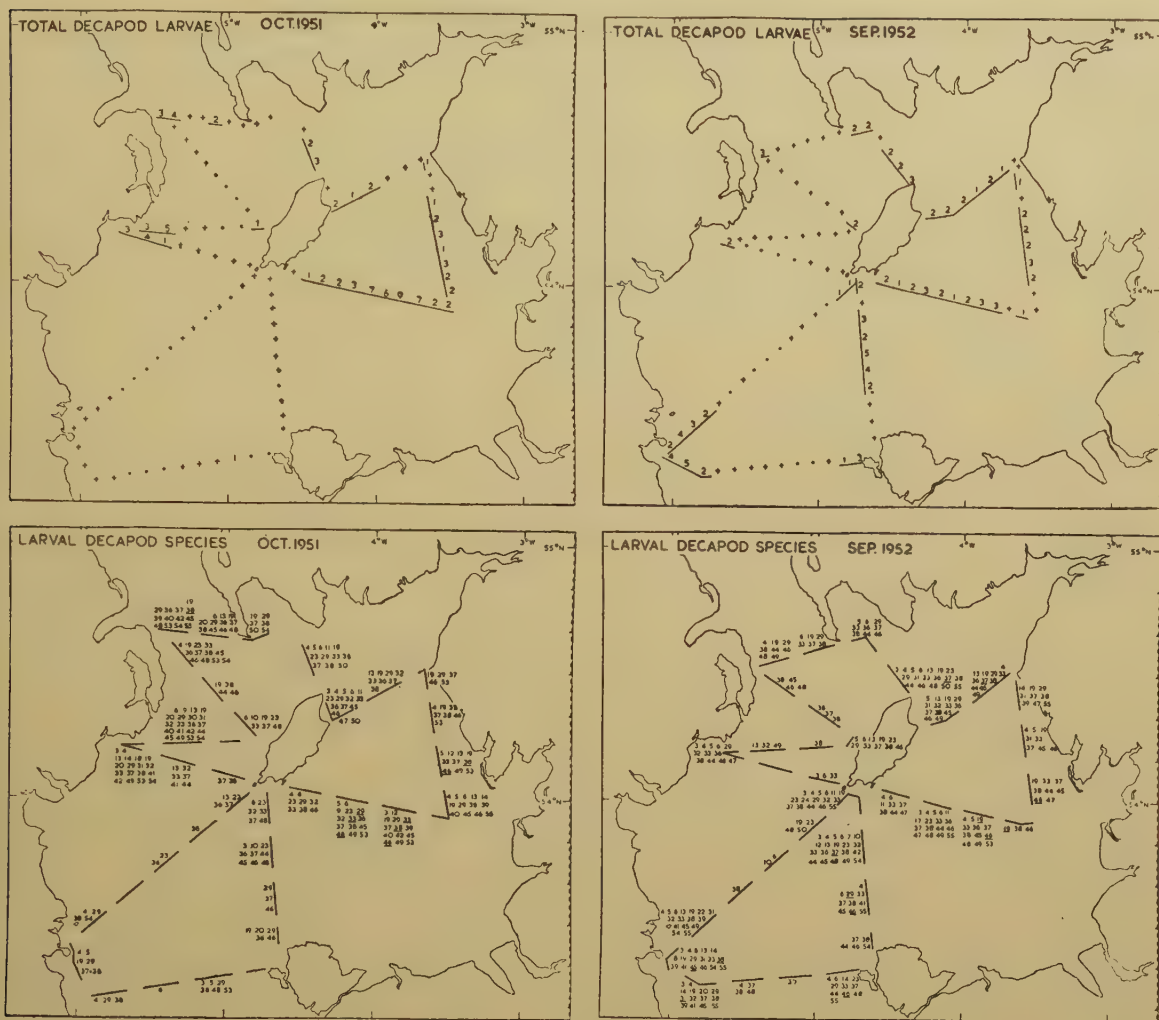
NYCTIPHANES
 O 1-9 10-99
 Cyrtopia • ◻
 Furcilia • ◐
 Calyptopis • ○

--- APPROX. LIMITS OF CYRTOPIA



Charts showing the distribution of total decapod larvae (upper row) in May 1951, and May 1952. The key refers to the numbers caught per 2-mile haul or approximately per 4 cu. metres of water filtered. The constituent species are indicated by the code numbers on the lower row of charts, which refer to the species given in the lists below this Plate and the one opposite. Greatest density per sample of each species in each group of samples given by: $n = 1-9$, $\underline{n} = 10-49$, $\boxed{n} = 50 +$.

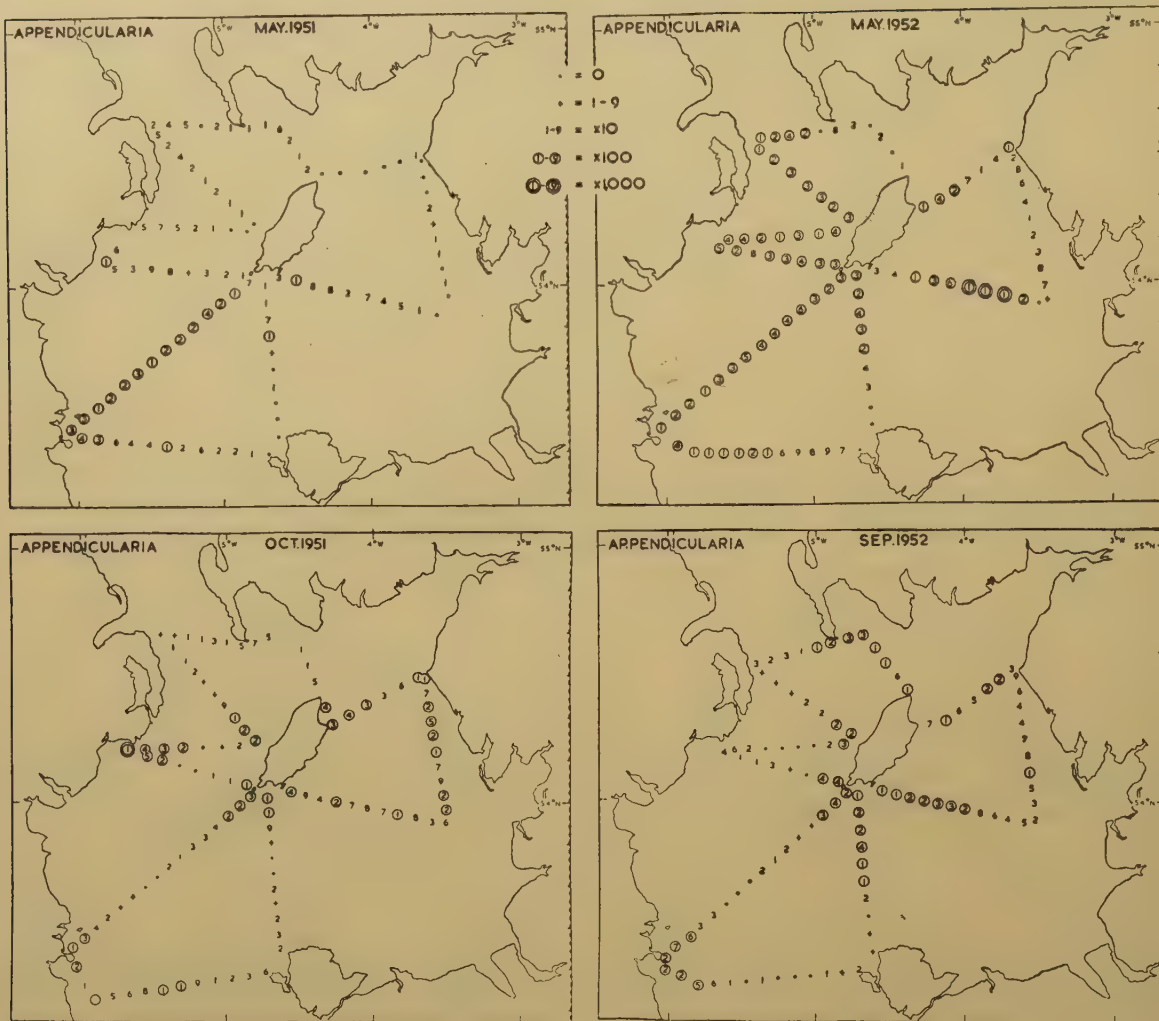
- | | |
|---|---|
| 1 <i>Pandalus montagui</i> Leach. | 14 <i>Crangon vulgaris</i> (L.) = <i>C. crangon</i> (L.). |
| 2 <i>Pandalus bonnierii</i> Caullery. | 15 <i>Crangon allmanni</i> Kinahan. |
| 3 <i>Pandalina brevisrostris</i> (Rathke). | 16 <i>Philocheras echinulatus</i> (Sars). |
| 4 <i>Hippolyte</i> spp. | 17 <i>Philocheras sculptus</i> (Bell). |
| 5 <i>Spirontocaris cranchii</i> (Leach). | 18 <i>Philocheras fasciatus</i> (Risso). |
| 6 <i>Spirontocaris occulta</i> Lebour. | 19 <i>Philocheras bispinosus</i> (Hailstone & Westwood). |
| 7 <i>Spirontocaris pusiola</i> (Krøyer). | 20 <i>Philocheras trispinosus</i> (Hailstone). |
| 8 <i>Spirontocaris gaimardi</i> (Milne-Edw.). | 21 <i>Pontophilus spinosus</i> (Leach). |
| 9 <i>Caridion gordonii</i> (Spence Bate). | 22 <i>Nephrops novaeigicus</i> (L.). |
| 10 <i>Alpheus ruber</i> Milne-Edw. | 23 <i>Galathea intermedia</i> Lilljeborg. |
| 11 <i>Athanas nitescens</i> (Montagu). | 24 <i>Galathea dispersa</i> Spence Bate. |
| 12 <i>Processa canaliculata</i> Leach. | 25 <i>Galathea nexa</i> Embleton. |
| 13 <i>Processa edulis</i> (Risso). | 26 <i>Galathea squamifera</i> Leach. |



Charts showing the distribution of total decapod larvae (upper row) in October 1951 and September 1952. The key refers to the numbers caught per 2-mile haul or approximately per 4 cu. metres of water filtered. The constituent species are indicated by the code numbers on the lower row of charts, which refer to the species given in the lists below this Plate and the one opposite. Greatest density per sample of each species in each group of samples given by: $n = 1-9$, $\bar{n} = 10-49$, $\bar{n} = 50 +$.

- 27 *Galathea strigosa* (L.).
- 28 *Munida bamffica* (Pennant).
- 29 *Porcellana longicornis* (L.).
- 30 *Porcellana platycheles* (Pennant).
- 31 *Jaxea nocturna* (Chiereghin).
- 32 *Callinassa* sp.
- 33 *Upogebia deltaura* Leach.
- 34 *Eupagurus bernhardus* (L.).
- 35 *Eupagurus pubescens* (Krøyer).
- 36 *Eupagurus prideauxi* (Leach).
- 37 *Anapagurus* spp.
- 38 *Portunus* spp.
- 39 *Carcinus maenas* (Pennant).
- 40 *Pirimella denticulata* (Mont.) ?
- 41 *Cancer pagurus* L.

- 42 *Atelecyclops septemdentatus* (Mont.).
- 43 *Corystes cassivelaunus* (Pennant).
- 44 *Pilumnus hirtellus* (L.).
- 45 *Gonoplax angulata* Pennant.
- 46 *Pinnotheres pisum* (Pennant).
- 47 *Pinnotheres pinnotheres* (L.) = *P. veterum* Bosc.
- 48 *Ebalia tuberosa* (Pennant).
- 49 *Ebalia cranchi* Leach.
- 50 *Maia squinado* (Herbst).
- 51 *Hyas araneus* (L.).
- 52 *Hyas coarctatus* Leach.
- 53 *Eurynome aspera* (Pennant).
- 54 *Inachus* spp.
- 55 *Macropodia longirostris* (Fab.).



Charts showing the distribution of Appendicularia in May 1951, May 1952, October 1951 and September 1952. The key refers to the numbers caught per 2-mile haul or approximately per 4 cu. metres of water filtered.

THE HARDY PLANKTON INDICATOR: A STUDY OF THE VARIATION BETWEEN CATCHES TAKEN BY DAY AND BY NIGHT.

BY

R. S. GLOVER, B.Sc.,¹ AND J. A. POPE, M.A.²

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INTRODUCTION.

THE Standard Plankton Indicator was designed by Professor A. C. Hardy (1926) to facilitate the study of the relationship between the catch of herrings and the plankton in the vicinity of the drift-nets. The investigations carried out during the Scottish, Northumbrian and East Anglian drift-net fisheries in 1930-34 showed a variable but generally positive correlation between the numbers of *Calanus* and the size of the catch of herrings (Hardy, Henderson, Lucas and Fraser, 1936).

While fishermen, for a number of reasons, have made little use of the Indicator as an aid to fishing, Gardiner (1933), Gibbons and Fraser (1937) and Williamson (1952) have used it for plankton surveys; and Fridriksson (1944) and Manteufel

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(1941) have also used it during investigations of the biological environment of the herring.¹ Einarsson (1951) tried the Indicator in Icelandic waters, but later changed to vertical hauls with a Hensen net when he observed that the Indicator appeared to collect more plankton by night than by day.

In 1947 work on the herring and its animate environment was resumed using a smaller version of the Hardy Indicator. The investigation was restricted to the north-east Scottish summer fishery which is based at Fraserburgh and Peterhead. A full description of the modified plankton Indicator, together with some discussion of its characteristics, is given by Glover (1953). Briefly, it consists of a copper tube fitted with diving planes. It is towed at a speed of about 8 knots, taking a horizontal haul at a depth of about 7 to 8 metres below the surface. Water is admitted at the front end through a hole of $\frac{1}{2}$ in. diameter and the plankton is filtered on to a silk disc with a diameter of $1\frac{1}{4}$ in. and with 60 meshes to the inch. The Indicator is towed for almost $1\frac{1}{2}$ miles during which, in theory, about one third of a cubic metre of sea water is filtered. The disc with its catch of plankton is removed and enclosed in a small envelope in which it is preserved over cotton-wool moistened with formaldehyde and returned to the laboratory for analysis.

In this new programme of work the Indicator is used in two ways to obtain data on plankton distribution over the fishing grounds.

Firstly, between 30 and 70 drift-net vessels, whose skippers are generous enough to co-operate, provide samples just before nightfall from the vicinity where they shoot their nets. Because of fishing habits these samples are all taken more or less simultaneously under similar conditions of light, tide and weather, but from a limited area. Secondly, the plankton over an area of more than 5000 square miles is sampled from the research ships of the Scottish Home Department which make regular surveys of the fishing grounds. The depth of the sea in this area ranges between 40 and 180 metres, but is mostly between 70 and 130. Such samples, taken as they are at fixed stations, are scattered in time throughout the 24 hours of the day. Consequently they may well be subject to variations resulting from the effect, at 8 metres below the surface, of vertical diurnal migrations of plankton.

Before drawing contours of plankton distribution it is necessary to assess the magnitude of such diurnal variations in order to compare the samples taken throughout the 24 hours from the research ships and those provided in the evening by the commercial vessels. There is also the possibility of seasonal changes in the vertical distribution of the plankton which will be reflected in both sources of data; these, however, would not necessarily prove a handicap to the main objective which is to compare the distribution of herring at any one time with the distribution of its main food organisms.

Our objectives were, therefore :

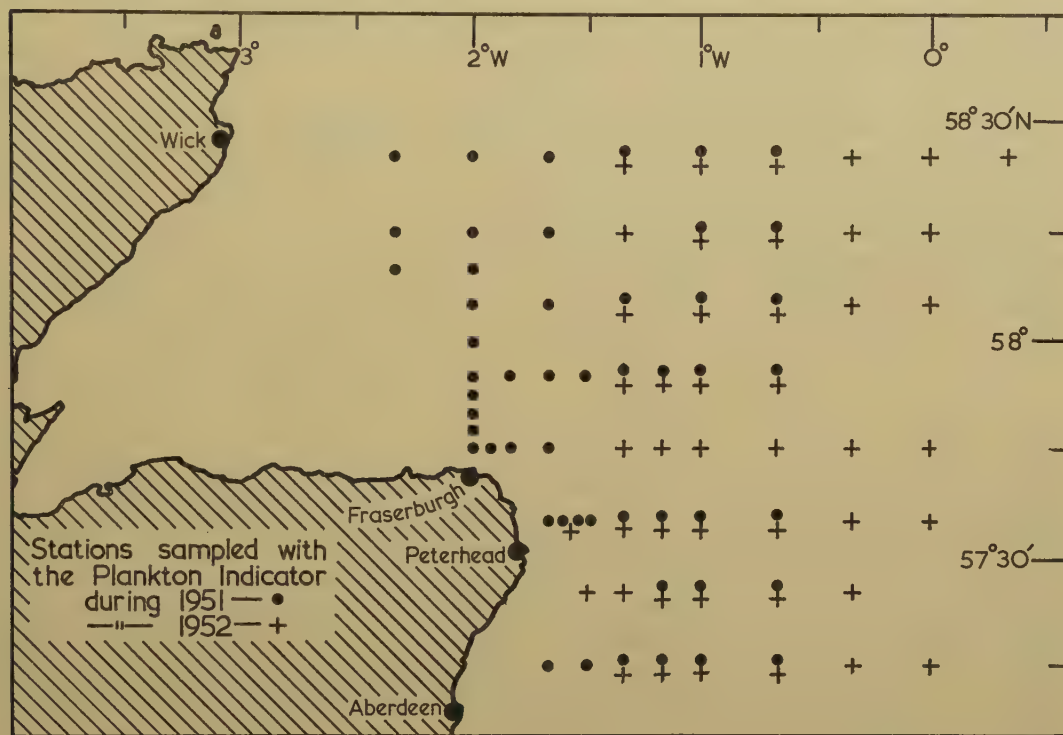
(a) To discover whether there was any evidence of a significant difference between Indicator samples taken during daylight and samples taken during darkness.

¹ Manteufel mentions that the instrument he used was a modified form of Hardy's Indicator but the nature of the modification is not described.

(b) If such an effect existed, to discover whether it was constant from cruise to cruise, and whether it is possible to calculate a correction factor by which the effect of night and day variations might be removed.

METHODS.

Each cruise lasted for some four to six days, during which samples were taken with the small Indicator at the stations shown in Text-fig. 1. The material collected from F.R.S. "Clupea" during the period April to August in the years 1951 and 1952 has been used in the analyses which follow.



TEXT-FIG. 1.—Chart showing the position of the stations which were selected for statistical analysis. See text, p. 119.

The plankton organisms were counted *in situ* on the silk discs from the Indicator. Five randomly spaced microscope fields provided a count of the phytoplankton lying on 1/120 of the whole disc. A single diametrical traverse of the disc provided a count of zooplankton organisms in 1/14 of the total sample. The counts in these sub-samples were used in the statistical analyses. In addition large animals, including copepodite stages V and VI of *Calanus finmarchicus*, were counted by eye, giving the total number present. In the counts of *Calanus* V and VI, therefore, there was no error introduced by sub-sampling in the laboratory. Besides stages V

and VI of *Calanus*, the groups used in the analyses which follow were *Calanus* stages I-IV, "Total Copepods" (the sum of all copepod species including *Calanus*) and "Total Dinoflagellates" (the sum of all species of *Ceratium*, *Dinophysis* and *Peridinium*).

In order to analyse the effect of diurnal variation the samples have been classified into two groups, (a) daylight samples taken between sunrise and sunset, and (b) night samples taken between sunset and sunrise.

The cruises were really designed as echo-sounding surveys with hydrographic sampling and vertical Hensen net hauls at each station. It was convenient to use the plankton Indicator at each of these stations; if the primary object of the cruises had been this study of diurnal variation of the Indicator catches, a more suitable experiment could have been designed and the statistical analyses would have been correspondingly easier to carry out.

In the present instance the analyses were complicated by two important factors. The number of stations which were visited varied from cruise to cruise, most cruises being incomplete due to adverse weather conditions. In addition the proportion of samples taken during daylight also varied from cruise to cruise. A straightforward application of the analysis of variance could not be made since inequality of the number of observations in the groups to be compared must be taken into account in a statistical analysis.

If x be taken as a general symbol for an observed count, the count obtained at the i^{th} station on the j^{th} cruise may be represented as x_{ijk} , where $k = 1$ or 2 according as the sample was taken during daylight or darkness. Now, the x_{ijk} 's are random variables distributed about true means X_{ijk} , these true means being a function of three main effects: station, cruise and time (day or night). In order to make valid tests of significance it is necessary that the x_{ijk} 's should, for all values of i , j and k , be normally distributed with constant variance about their true means.

It is a characteristic of plankton sampling, however, that the variance of a count is not constant but increases more or less linearly with the square of the mean level. Stability of variance may, however, be achieved by making an appropriate change of scale.¹ In the present instance a transformation $y = \log_{10}(x + 1)$ was used. It seems reasonable to suppose that on this scale the transformed observations (y) may be represented, to a good approximation, as a linear function of constants representing the effect of specific factors which can be estimated from the data, together with a random term due to unascrivable variation. That is, we may write

$$y_{ijk} = m + s_i + c_j + t_k + (ct)_{jk} + z_{ijk}$$

where m = a constant representing the overall true mean of the counts;
 s_i = a constant representing the added effect of the i^{th} station;
 c_j = a constant representing the added effect of the j^{th} cruise;
 t_k = a constant representing the added effect of time (day or night);

¹ For an account of the use of transformations, see Quenouille (1950a). See also the review by Barnes (1952).

$(ct)_{jk}$ = a constant representing the interaction of the j^{th} cruise with daylight or darkness ;

z_{ijk} = a random variable, independently and normally distributed with zero mean and constant variance, representing the uncontrolled or "error" variation.

The inclusion of constants $(ct)_{jk}$ for interaction is necessary in order to test whether the effect of time of sampling on the counts is constant from cruise to cruise. If the constants $(ct)_{jk}$ are not significant the day and night effect may be regarded as the same on all cruises, and an estimate of the average effect of daylight and darkness over all cruises can be obtained. On the other hand, when the constants $(ct)_{jk}$ are not zero we are led to study the effect of day and night for each separate cruise.

The values of the constants involved in the proposed model may be estimated by the method of least squares ; that is, by minimizing the sum of squares of the errors z_{ijk} .¹ Owing to the large number of constants involved this approach is unmanageable here.

As the primary objective was to test the effect of day and night, it was unnecessary to estimate all the constants and their variances and covariances explicitly. Instead the proposed model was fitted by an extension of the analysis of variance technique suggested by Quenouille (1950b).

RESULTS.

A certain amount of selection of the material was carried out prior to analysis. Thus some cruises were so interrupted by adverse weather conditions that the small amount of information furnished by them did not warrant their inclusion in the analyses. Stations which were visited less than three times during the series of cruises in any one year were also discarded. This selection of data led to no bias in the conclusions reached. The dates of the cruises which were used are shown below, the number of samples used from each cruise being given in brackets.

1951.			1952.		
Cruise	1 : April 24th-26th	(27)	Cruise	1 : April 14th-18th	(32)
	2 : May 7th-12th	(38)		2 : April 28th-May 2nd	(35)
	3 : May 21st-24th	(33)		3 : May 12th-16th	(36)
	4 : June 4th-7th	(36)		4 : June 1st-6th	(43)
	5 : June 18th-21st	(51)		5 : July 21st-25th	(33)
	6 : July 9th-12th	(42)		6 : August 4th-8th	(39)
	7 : July 23rd-26th	(39)		7 : August 18th-22nd	(40)
	8 : August 6th-9th	(32)			
	9 : August 21st-24th	(25)			
	10 : August 28th-29th	(12)			

¹ For a theoretical account of the least-squares approach in the analysis of variance see, for example, Anderson and Bancroft (1952).

Because of the disproportionate numbers in the various classifications of the data, the separate sums of squares due to stations, cruises, and time, in each case eliminating the effects of the other two, do not add up to the sum of squares corresponding to the degrees of freedom for these main effects together.

On any single cruise, as one would expect, there were gross changes in the abundance of plankton from station to station, and between groups of stations, even after allowing for time of day. This being so, a non-significant sum of squares for stations merely implies that the distribution of plankton in space was not consistent throughout the period covered by the successive cruises.

In the tables which follow, the notation used is

C = cruises ;
 S = stations ;
 T = time (day or night) ;
 $C \times T$ = interaction of cruises and time.

Levels of significance are denoted by asterisks. One asterisk denotes significance at the 5% level of probability ; two asterisks denote significance at the 1% level ; and three asterisks denote significance at the 0.1% level.

Calanus, Copepodite Stages V and VI.

The analysis of variance of the 1951 samples is given in Table I.

TABLE I.—*Analysis of Variance of Calanus V and VI, 1951 Survey.*

	d.f.	s. of s.	m.s.	v.r.
S (eliminating C and T)	50	12.4732	0.2495	—
C (eliminating S and T)	9	24.9145	2.7683	11.68***
T (eliminating S and C)	1	0.1894	0.1894	—
S + C + T	60	43.0053	—	—
$C \times T$ (eliminating S)	9	9.0135	1.0015	4.22***
Residual	265	62.8296	0.2371	—
Total	334	114.8484		

The significance of the $C \times T$ interaction shows that the effect of day and night was not constant from cruise to cruise. The ratios of night counts to day counts for each cruise are shown in Table II, where it will be seen that night counts were higher than day counts in the middle of the season with a reversal at the beginning and end.

TABLE II.—*Ratio of Night Counts to Day Counts, Corrected for Station Effects, of Calanus V-VI during 1951 Survey ; figures in italics indicate a significant difference from unity.*

Cruise.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
Ratio	0.6	0.6	1.0	1.4	2.0	1.6	2.5	1.2	0.7	0.4

*

However, only on one cruise, number 7, was the ratio significantly different from unity.

A different result for the 1952 samples of *Calanus* V–VI was found. The analysis of variance of the 1952 data, given in Table III, shows a highly significant effect of time on the counts, and since the $C \times T$ interaction fails to reach significance at the 5 % level, the effect of day and night in this case may be regarded as being constant from cruise to cruise.

TABLE III.—*Analysis of Variance of Calanus V and VI, 1952 Survey.*

	d.f.	s. of s.	m.s.	v.r.
S (eliminating C and T)	44	14·1141	0·3208	—
C (eliminating S and T)	6	22·6031	3·7672	15·68***
T (eliminating S and C)	1	4·3561	4·3561	18·13***
S + C + T	51	43·4670	—	—
$C \times T$ (eliminating S)	6	2·8802	0·4800	—
Residual	200	48·0518	0·2403	—
Total	257	94·3990		

The average ratio of night counts to day counts for the whole season, corrected for cruise and station effects, was found to be 2·1, a value differing significantly from unity ($P < 0·001$). The 95% confidence limits for this ratio are 1·5 and 3·0.

The ratio of night counts to day counts for each cruise are shown in Table IV.

TABLE IV.—*Ratio of Night Counts to Day Counts, corrected for Station Effects, of Calanus V–VI during 1952 Survey; figures in italics denote a significant difference from unity.*

Cruise.	1.	2.	3.	4.	5.	6.	7.
Ratio	2·4	3·2	2·4	2·2	1·5	2·2	0·9
	*	*	*	*		*	

Calanus, Copepodite Stages I–IV.

The analysis shown in Table V indicates the existence of a highly significant effect of day and night on the 1951 counts of *Calanus* I–IV ($P < 0·001$). In addition the $C \times T$ interaction is significant ($P < 0·001$).

TABLE V.—*Analysis of Variance of Calanus I–IV, 1951 Survey.*

	d.f.	s. of s.	m.s.	v.r.
S (eliminating C and T)	50	9·6119	0·1922	—
C (eliminating S and T)	9	5·1626	0·5736	3·93***
T (eliminating S and C)	1	3·2321	3·2321	22·15***
S + C + T	60	17·5526	—	—
$C \times T$ (eliminating S)	9	4·7698	0·5300	3·63***
Residual	265	38·6745	0·1459	—
Total	334	60·9969		

This indicates that the time effect was not constant from cruise to cruise. Only on cruises 5, 6 and 7 did the night and day counts differ significantly, the night counts being higher than day counts on these cruises. The ratios of night counts to day counts, corrected for station effects, are given in Table VI for each cruise.

TABLE VI.—*Ratio of Night Counts to Day Counts, Corrected for Station Effects, of Calanus I-IV during 1951 Survey; figures in italics indicate a significant difference from unity.*

Cruise.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
Ratio	1.1	1.2	1.2	1.3	2.4 **	3.8 ***	4.3 ***	1.0	0.6	0.8

The analysis summarized in Table VII gives similar results for the 1952 material; the effect of day and night on the counts of *Calanus* I-IV in 1952 was significant, the magnitude of the effect varying from cruise to cruise.

TABLE VII.—*Analysis of Variance of Calanus I-IV, 1952 Survey.*

	d.f.	s. of s.	m.s.	v.r.
S (eliminating C and T)	44	8.0236	0.1824	—
C (eliminating S and T)	6	13.8023	2.3004	17.99***
T (eliminating S and C)	1	2.6974	2.6974	21.09***
S + C + T	51	23.7989	—	—
C × T (eliminating S)	6	2.9175	0.4862	3.80**
Residual	200	25.5884	0.1279	—
Total	257	52.3048		

The ratios of night counts to day counts are shown in Table VIII. Counts in samples taken at night were significantly larger than in those taken by day on cruises 2, 3 and 4, the observed differences on other cruises being non-significant.

TABLE VIII.—*Ratio of Night Counts to Day Counts, Corrected for Station Effects, of Calanus I-IV during 1952 survey; figures in italics indicate a significant difference from unity.*

Cruise.	1.	2.	3.	4.	5.	6.	7.
Ratio	1.0	3.1 ***	4.2 ***	1.8 *	1.2	1.3	1.2

Total Copepods.

The analysis of variance of the 1951 samples of Total Copepods is given in Table IX.

The effect of day and night on the sample counts was found to be highly significant ($P < 0.001$), but the existence of a significant $C \times T$ interaction shows that this effect was not constant on all cruises. Further analysis showed that night counts were significantly lower than day counts on cruise 1 and night counts were

TABLE IX.—*Analysis of Variance of Total Copepods, 1951 Survey.*

	d.f.	s. of s.	m.s.	v.r.
S (eliminating C and T)	50	9.1334	0.1827	—
C (eliminating S and T)	9	39.9158	4.4351	25.80***
T (eliminating S and C)	1	4.6766	4.6766	27.21***
S + C + T	60	58.6569	—	—
C × T (eliminating S)	9	6.7342	0.7482	4.35***
Residual	265	45.5442	0.1719	—
Total	334	110.9353		

significantly higher than day counts on cruises 5, 6, 7 and 8. The ratios of night counts to day counts are shown in Table X.

TABLE X.—*Ratio of Night Counts to Day Counts, Corrected for Station Effects, of Total Copepods during 1951 Survey; figures in italics indicate a significant difference from unity.*

Cruise.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
Ratio	0.3	0.7	1.7	0.8	2.6	2.8	5.2	2.3	0.7	0.7
	**				**	**	***	*		

In 1952 the effect of daylight and darkness on the counts of Total Copepods was highly significant ($P < 0.001$). The $C \times T$ interaction was found to be non-significant. That is, the effect of day and night could be regarded as constant for all cruises. Over the whole season, the average ratio of night counts to day counts, corrected for station and cruise effects, was found to be 2.5 with 95% confidence limits 1.9 and 3.4. The analysis of variance is shown in Table XI.

TABLE XI.—*Analysis of Variance of Total Copepods, 1952 Survey.*

	d.f.	s. of s.	m.s.	v.r.
S (eliminating C and T)	44	10.6282	0.2416	—
C (eliminating S and T)	6	6.8787	1.1464	6.39***
T (eliminating S and C)	1	6.7253	6.7253	37.49***
S + C + T	51	28.7626	—	—
C × T (eliminating S)	6	0.0489	0.0082	—
Residual	200	35.8836	0.1794	—
	257	64.6951		

The ratios of night counts to day counts for each cruise are shown in Table XII.

TABLE XII.—*Ratio of Night Counts to Day Counts, Corrected for Station Effects, of Total Copepods during 1952 Survey; figures in italics denote a significant difference from unity.*

Cruise.	1.	2.	3.	4.	5.	6.	7.
Ratio	1.4	3.3	3.6	1.5	1.9	2.4	1.2
		***	***		**	***	

Dinoflagellates.

The analyses of the counts of dinoflagellates for both the 1951 and 1952 surveys are shown in Table XIII. As was to be expected, a preliminary examination of the material suggested that daylight and darkness had no effect on the counts on any of the cruises and in the analyses it was decided not to remove the interaction sum of squares. As very few dinoflagellates were encountered on the first two cruises of 1952, these cruises were omitted.

TABLE XIII.—*Analysis of Variance of Dinoflagellates.*

(a) 1951 Survey,					
	d.f.	s. of s.	m.s.	v.r.	
S (eliminating C and T)	50	25.4658	0.5093	—	
C (eliminating S and T)	9	100.9132	11.2126	45.84***	
T (eliminating S and C)	1	0.7389	0.7389	—	
S + C + T	60	148.3074	—	—	
Residual	274	67.0248	0.2446	—	
Total	334	215.3322			

(b) 1952 Survey,					
	d.f.	s. of s.	m.s.	v.r.	
S (eliminating C and T)	44	6.2786	0.1427	—	
C (eliminating S and T)	4	29.5471	7.3868	36.35***	
T (eliminating S and C)	1	0.0057	0.0057	—	
S + C + T	49	39.5170	—	—	
Residual	141	28.6562	0.2032	—	
Total	190	68.1732			

Table XIII shows that there was no overall effect of day and night on the counts in either year.

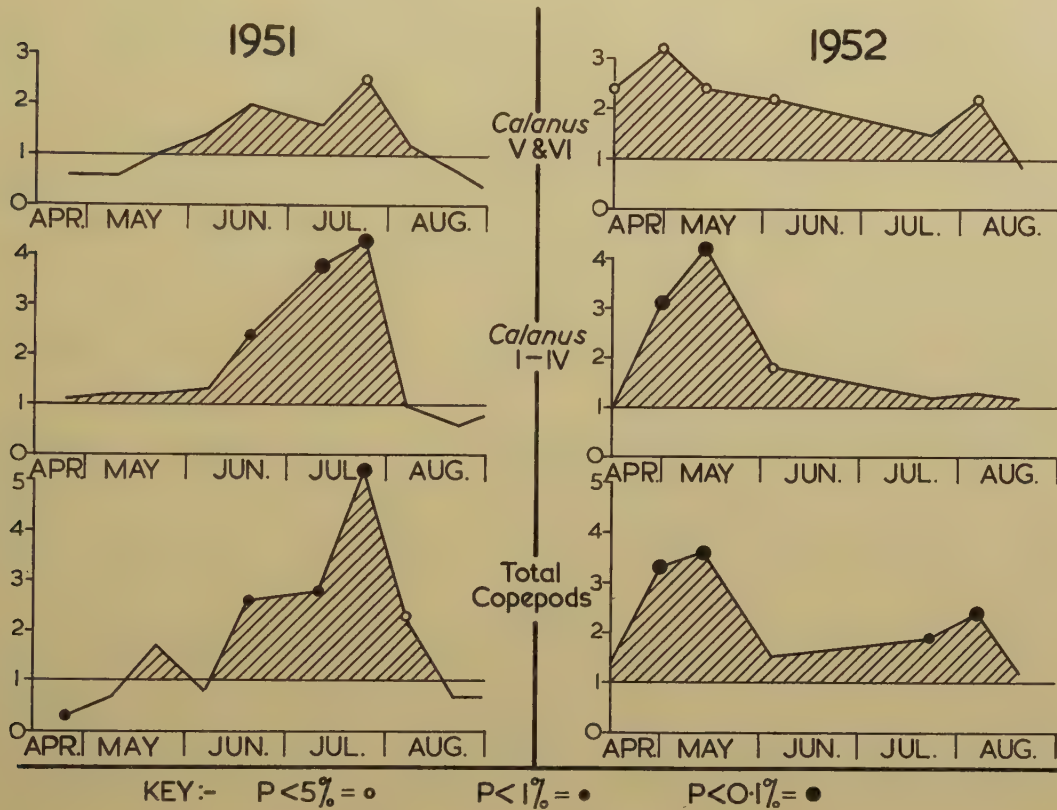
ON THE INTERPRETATION OF THE RESULTS.

The numbers of dinoflagellates showed no sign of diurnal variation. This was to be expected in the open sea although Hasle (1950 and 1954) has found diurnal vertical migration of dinoflagellates in the sheltered waters of the inner Oslo Fjord.

The results for large and small *Calanus* and for Total Copepods, on the other hand, showed that there were often significant differences between samples taken by night and those taken by day. The results are shown in Text-fig. 2 in the form of the ratio of night catches to day catches; of 51 ratios, 21 show a significant departure from unity, night catches being higher than day catches for all but one of these 21 results.

Seasonal Variations.

The difference between night and day catches was not constant from cruise to cruise within each season. The seasonal variations were not, however, significant in 1952 for the groups *Calanus* V and VI and Total Copepods of which, on average, about twice as many were taken during the night than by day throughout the season.



TEXT-FIG. 2.—Graphs showing, for each cruise, the ratio of night to day catches with the small plankton Indicator, corrected for station effects. The vertical scale shows the fraction “night counts divided by day counts.” The hatched area indicates the period when this fraction was greater than 1.0, *i.e.* when more copepods were taken by night than by day. The points on the graphs are marked by symbols which represent the significance of the difference between night and day catches according to the values given in the key.

From cruise to cruise there were highly significant variations of the night/day ratios for all three copepod groups in 1951 and for *Calanus* I-IV in 1952. From the graphs of these groups in Text-fig. 2 it is clear that the night/day ratios tended to be high in the middle of each season and low at the beginning and end of each season. Indeed twelve results suggest that catches were greater by day than by night;

although this was significant only for Total Copepods in April, 1951, the consistency of the effect is apparent.¹

Although these results may suggest increased vertical migration in mid-summer, they might also be explained on the grounds of gross changes in the overall, or residual, vertical distribution of the copepods at different times of the year. Russell (1928) noticed that there was a seasonal descent of *Calanus* from a depth of about 10 metres, in April, to about 20 metres in June, followed by a rise towards the surface in July, August and September. Marshall, Nicholls and Orr (1934) found that from March until the end of May, *Calanus* stages V and VI in Loch Striven inhabited the upper ten metres "continuously and exclusively". Thereafter in their daylight surveys, which extended into late August, these stages were seldom found above 10 metres. That such a seasonal cycle in Loch Striven is not restricted to *Calanus* is shown by Marshall (1949) who demonstrated that, from the end of March until the middle of June, the great majority of all stages of all the small copepods except *Microcalanus* was above 10 metres. In July most stages of all species were below that depth, and in August most species, more particularly the younger stages, showed a gradual rise towards the surface again. When the survey of Loch Striven ended on August 21st the small copepods had not quite returned to the distribution, above 10 metres, which was found in March.

Sinking of the over-wintering individuals to the greatest depths has been described by many workers (see Russell, 1935, for references). In the same area as the present survey, Gibbons (1936) has shown a progressive sinking of *Calanus* from March to October. But his results also suggest a spring and autumnal rise of some individuals to the surface ; this is superimposed on the general descent to the bottom as winter approaches.

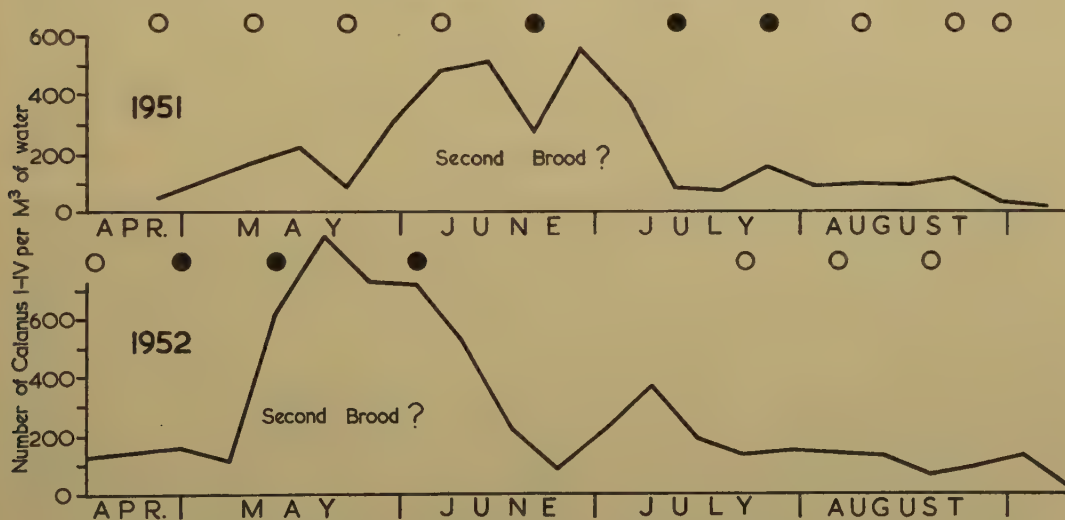
Moore, Owre, Jones and Dow (1953), using samples from 10 miles east of Miami, found a similar seasonal variation in the level of the population ; their results show that the copepods were deepest in May and June, and were nearest the surface in December.

One may suppose, therefore, that at the beginning and end of each Scottish east coast fishing season, the centre of abundance of most copepod species may lie, during the daytime, somewhere near the level of Indicator sampling, about 8 metres, and that during the night they tend to rise above the Indicator level. In the middle of the season, however, the majority of the copepods may lie below the Indicator by day and may rise into the sampling level by night. The mid-summer nights being relatively light, and assuming that illumination is the limiting factor, the copepods may not rise into the superficial levels above the Indicator, as they are presumed to do in the spring and autumn. This hypothesis might help to explain the differences between 1951 and 1952 which are apparent in Text-fig. 2. The same seasonal pattern

¹ Barnes (1953), using the Continuous Plankton Recorder at a depth of 10 metres in the Clyde Sea, found that a number of organisms, including the copepods *Acartia clausi* and *Paracalanus parvus* were more numerous in samples taken by day than by night. Since his samples were taken in early May, this finding is in agreement at least with the results obtained with the Indicator in 1951.

was followed in both years ; the night/day ratios were small at the beginning and end of each season and were large in the middle of the season. A major difference, consistently reflected by all three groups of organisms, was that the incidence of bigger catches by day than by night in 1951 was not so marked in 1952. On the above hypothesis, this result might be expected if a similar sequence of biological events occurred in both years but, in 1952, the copepods tended to live deeper in the water than in 1951.

Marshall *et al.* (1934) concluded that the first *Calanus* brood of each season lived above, and the second brood lived below 10 metres ; in the quite different conditions of Miami, Moore and his co-workers (1953) suggested that the seasonal cycle of the "mean depth" of the copepod population might be correlated with the succession of broods. It is notable, therefore, that in the present work, the period when night catches of young *Calanus* were significantly higher than day catches was much later in 1951 than in 1952. The indicator samples taken during early evening by fishermen show that the peak numbers of *Calanus*, stages I-IV, which are interpreted as representing the appearance of a brood, were also later in 1951 and roughly coincided with the period of significantly high night catches in both years (see Text-fig. 3). Since Rees (1949, his Text-fig. 12) suggested that the first brood of *Calanus* probably appears before the herring survey begins in May, it may be inferred that the brood which was more numerous in the Indicator by night and which on the above hypothesis was living below 10 metres during the day, was the second brood which Marshall, Nicholls and Orr also found to be deep-living.



TEXT-FIG. 3.—Graphs showing, week by week, the average number of *Calanus* I-IV per cubic metre of water sampled. The material was collected from the area shown in Text-fig. 1, by fishermen using the small plankton Indicator just before the drift-nets were shot. Circles above each graph indicate the dates of research ship cruises for which night/day ratios have been calculated; these blacked-in show the occasions when night catches were significantly greater than day catches; open circles indicate that the difference between night and day was not significant.

Comparison with Previous Work.

The vertical migrations of *Calanus* in the waters off north-east Scotland were investigated by Gibbons (1936). He took series of three horizontal hauls with cheesecloth townets at the surface, "at about mid-water" and near the bottom. From these he was able to estimate the numbers and relative proportions of *Calanus* at the three depths. He concluded "that the maximum diurnal migrations occur at those seasons when the hours of darkness are longest, while in July, when the light is strong, even at a late hour, the difference between daylight and dark hauls is least marked". Gibbons remarked that this result conflicted with the work of Nicholls (1933) and Russell (1935), both of whom concluded that diurnal vertical migration was minimal in the winter. Gibbons infers (1936, p. 14) that one explanation of these opposing conclusions was that Nicholls and Russell took their material from a different area; conditions might be different off N.E. Scotland.

Gibbons' material has been re-examined, since the collections for the present work were taken from approximately the same area as that sampled by him.

Gibbons' inference was based on the division of the numbers of *Calanus* in night samples by the numbers in day samples in his surface collections only.¹ In his final result he does not distinguish between the copepodite stages of *Calanus*; probably few young stages were caught with his cheesecloth nets. However, from the detailed tables (Gibbons, 1936, pp. 7-12) it is possible to calculate the numbers of "mature" *Calanus* in each haul. These were mostly stage VI females and approximate to the group "*Calanus* V and VI" used in the present work. The results of the transformation of Gibbons' data are seen in Text-fig. 4. The results for April and June have been excluded because nearly all the material in those months was taken from the Atlantic. Gibbons combined the material for February and March; because there were relatively few samples, the results for October and November have also been combined in the present treatment.

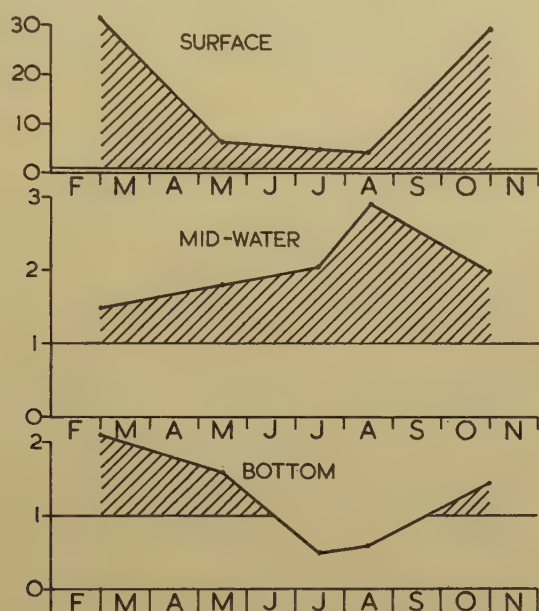
In the surface and mid-water hauls, more *Calanus* were caught by night than by day throughout the period of the investigations. At the surface, where *Calanus* was least abundant, the difference between night and day catches was most marked in spring and late autumn. But the mid-water samples showed the reverse; the difference between night and day samples was most marked in July and August. The Indicator samples and Gibbons' mid-water material, therefore provide similar results. The ratio of night to day catches of *Calanus* V and VI increased to $\times 2.5$ in late July 1951 in the Indicator collections and to $\times 2.9$ in August in Gibbons' material. In 1952 the ratios of night to day catches of *Calanus* V and VI did not differ significantly from cruise to cruise, but the 95% confidence limits for the whole

¹ He expressed the catches of his surface nets as the percentage of the total at all three depths. The percentage at the surface by night was then divided by the percentage at the surface by day. A similar result is achieved by dividing the actual numbers of *Calanus* caught at night by those caught during daylight; Gibbons' figures are here expressed in the latter way to conform with the technique used in the present paper.

season were $\times 1.5$ to $\times 3.0$ compared with the range, $\times 1.8$ to $\times 2.9$, shown by Gibbons' results from mid-water during May to August.

In July and August the bottom nets caught more *Calanus* by day than by night ; this might be expected if vertical migrations were most marked at this time and most of the *Calanus* had, during the night, risen above the level of the bottom net.

It is difficult, however, to interpret this type of material in terms of the varying extent of vertical migration. Gibbons' mid-water hauls and the Indicator samples at 8 metres both show the same effects, whether these result from seasonal variations of vertical migration or from variations of the mean depth of the population. One difference between the two investigations is that the Indicator caught fewer *Calanus*



TEXT-FIG. 4.—Graphs, derived from data published by Gibbons (1936), showing the ratio of night to day catches of "mature" *Calanus* taken in horizontal hauls with cheesecloth nets. The vertical scale gives the fraction "night counts divided by day counts." The hatched area indicates the period when more *Calanus* were taken by night than by day.

by night than by day during spring and autumn, whereas Gibbons' nets always caught more by night. It is possible that *Calanus* can escape slow moving nets, particularly by daylight, whereas they are less likely to escape the Indicator travelling at 8 knots. It may be that the relatively large differences between night and day which Gibbons found at the surface resulted partly from the greater ability of copepods to escape the net by day in the well-lit surface waters compared with the conditions at greater depths.

There are other reasons for believing that it is unlikely that conditions at the surface would fairly reflect the mass movements of the *Calanus* population. In particular, it seems probable that many copepods, even when they are performing

vigorous vertical migrations, only approach the actual surface when the night is very dark. As Gibbons remarks, in northern Scotland the light is strong even at a late hour during the summer. Gibbons' results, like those of the other workers discussed above, suggest some general shift towards the surface in spring and autumn. The surface of the sea forms a boundary to the migrations of marine animals, regardless of the position of the optimum light intensity. Upward migrations of the slightest extent by a superficial population might, as a result of aggregation compelled by the proximity of the surface, produce a most marked difference between day and night samples. It is possible, therefore, that Gibbons' material does not, as he supposed, conflict with the earlier findings of Nicholls (1933) and Russell (1935). Certainly, Gibbons' and the present work suggest that, in horizontal hauls in the intermediate depths, the effects of diurnal vertical migrations of *Calanus* were maximal in mid-summer.

General Remarks.

As a matter of expediency and because the Indicator samples were primarily part of a large scale herring-plankton survey, no distinction was made between stage V and stage VI *Calanus*, or between the "finmarchicus" and "helgolandicus" forms described by Rees (1949). Examination of a proportion of the group *Calanus* V and VI showed that only about 3 % were of the form "helgolandicus".¹ There was no evidence of seasonal or diurnal differences in the proportions of the two forms of *Calanus*. The results and conclusions described here refer, therefore, almost entirely to *Calanus finmarchicus* (Gunn.), form "finmarchicus".

Inspection of a further sub-sample suggested that some of the seasonal changes in the ratio of night to daylight catches of "*Calanus* V and VI" might be attributable to a difference between the behaviour of stage V and stage VI. The evidence is somewhat slender, however, and further work is required to resolve this point.

Further work is also necessary before an explanation can be offered of the fact that the night/day ratios of *Calanus* V and VI and of Total Copepods showed significant seasonal variations in 1951 but not in 1952. Variations in the proportion of copepodite stages of *Calanus* and of the different species of copepods might be responsible; changes in the general level of the populations in different years as well as a difference in the magnitude of diurnal vertical migration must also be considered.

It is partly to study such questions as these that, during 1954, five plankton Indicators have been towed simultaneously at depths from 2 to 30 metres.

Finally, it should be emphasized that, seasonal variations apart, the fact that for long periods there was no significant difference between the catches by day and by night at 8 metres need not be surprising. Such a fact does not imply that diurnal migration was not taking place, but only that its effect was not noticeable at a particular depth. Rae and Fraser (1941) concluded from a series of horizontal net

¹ We are indebted to Dr. C. B. Rees for this information.

hauls, taken at various depths by Savage (1931), that in the shallow waters of the southern North Sea, the perceptible effect of vertical migration in the Continuous Plankton Recorder catches of copepods at 10 metres would be negligible in relation to other sources of variation. Barnes (1953) confirmed this point for a number of species by experiments with the Recorder in the Clyde Sea area.

However, the results from the plankton Indicator, used in the northern North Sea, show that there was sometimes a significant difference between night and day catches. It is clear, from the preceding analyses, that there is no universally applicable correction factor by which catches taken by day may be multiplied to equate them with night catches. If night/day ratios are to be used to correct day catches, then a different multiplier is required for each cruise and for each organism. Further, the arbitrary division into day and night sampling is only a first approximation in analysing the effect of time of day. Cushing (1951), who has reviewed work on vertical migrations of plankton, suggests that the cycle can be divided into four phases: (a) ascent from the day depth; (b) midnight sinking; (c) dawn rise; (d) descent to the day depth. Many workers have shown that this pattern will be modified by variations of atmospheric conditions and that the speed of movement of planktonic animals differs with varying light intensity.

More recently, Moore, Owre, Jones and Dow (1953) have studied the vertical distribution of pteropods, siphonophores, chaetognaths and copepods during the daytime only. They showed that the vertical spread of these organisms was influenced by light at its upper level, but that temperature was the controlling factor at greater depths. Lewis (1954) also has shown that light and temperature influence the vertical distribution of euphausiids during the daytime in the Florida Current, but he concludes that the distribution during the night is under the control of light.

It is clear, therefore, that even if the 24-hour period had been divided into a greater number of groups than the two (night and day) used here, the more detailed results could not be used to deduce correction factors for future sampling with the plankton Indicator. Whether the larger variations, exceeding $\times 2$, can be neglected, or whether they will affect the overall picture of the plankton in the current investigations must be decided in the light of the plankton gradients which are found. This point will be discussed in a subsequent paper dealing with the distribution of the plankton.

SUMMARY.

1. The small plankton Indicator was used in 1951 and 1952 from April to August during surveys of the herring fishery off north-east Scotland. The samples, taken 8 metres below the surface, have been used to study the diurnal variability of catches of copepods which presumably results from differences in the vertical distribution of the plankton.

2. Analysis of the results shows that, although more copepods were usually taken by night than by day, the effect was not uniform throughout each season.

The difference between night and day catches tended to be greatest in mid-summer. In spring and autumn the difference was slight and sometimes reversed when more copepods were taken by day than by night.

3. It is suggested that seasonal variations of the difference between night and day catches in plankton Indicator hauls may result from two phenomena which have been described by other workers :

- i. Diurnal vertical migration is probably maximal in mid-summer.
- ii. The superficial population of copepods probably retreats from the surface during the summer.

In spring and autumn a majority of the copepods may lie near the Indicator depth (8 metres) during the day and may rise above this level at night. In summer most of the copepods are presumed to live below 8 metres by day and to rise to this level at night.

4. Results published by Russell, Marshall, Nicholls and Orr lend support to this explanation. The data published by Gibbons have been re-examined ; it is suggested that, contrary to the implications of Gibbons, his material does not conflict with their findings.

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NOTES ON THE DIFFERENCES BETWEEN *CALANUS FINMARCHICUS* (GUNN.) AND *CALANUS* *HELGOLANDICUS* (CLAUS).

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FOR many years the question of whether the two forms, *Calanus finmarchicus* (Gunn.) and *Calanus helgolandicus* (Claus), could be distinguished satisfactorily was in doubt. For example, Sars (1903), Wilson (1932) and Rose (1933) believed the two forms to be distinct, Giesbrecht (1892), Wolfenden (1904) and Gough (1905) thought otherwise. Many other systematists have commented on what appeared to be minor morphological differences of doubtful significance, such as overall length, body proportions, the profile of the anterior margin of the cephalosome, the denticulation on the basipodite of the 5th leg, and the asymmetry of the 5th pleopod in the male.

However, Rees (1949) demonstrated a clear diagnostic feature which had not previously been emphasized. The inner margin of the proximal segment of the 5th leg was more concave in *helgolandicus* than in *finmarchicus* and it carried fewer and heavier teeth. He pointed out that this feature invariably confirmed his identifications based on the profile of the anterior margin of the animal and that with experience a worker could differentiate between the two forms on this latter character alone in nearly all cases. Later, however, Marshall, Orr and Rees (1953) drew attention to an intermediate form. A number of specimens found near Tromsø showed a tooth arrangement between those of the *finmarchicus* and *helgolandicus* types, but a head profile similar to that of the former.

The characters suggested by Rees proved satisfactory in samples taken from the North Sea (Samples I and II in Table I) although a few individuals of doubtful

TABLE I.

Sample No.	Date.	Position.	Number of specimens.	
			<i>C. finmarchicus.</i>	<i>C. helgolandicus.</i>
I	January 14th, 1953	56° 20' N. 00° 50' E.	179	37 ⁽¹⁾
II	January 16th, 1953	55° 50' N. 00° 40' W.	225	94 ⁽²⁾
III	June 12th, 1953	58° 55' N. 03° 47' W.	169	—
IV	April 16th, 1953	61° 01' N. 01° 00' W.	490	100
V	January 16th, 1953	55° 20' N. 01° 30' E.	—	163
VI	January 16th, 1953	55° 20' N. 00° 20' E.	—	251

⁽¹⁾ plus 5 specimens of doubtful affinity.

⁽²⁾ plus 11 specimens of doubtful affinity.

affinity were again found; 221 and 330 adult females were examined, respectively, in two samples. Only five in Sample I and eleven in Sample II could not be readily attributed to one or other profile type; they had a profile which appeared to be intermediate between the two types. Next, the tooth arrangement on the basal joints of the 5th pleopods were examined in each individual and in no case did the identification conflict with that based on the cephalosome profile. But here again a few intermediates were found, including all those showing doubtful affinities in the profile and also a few specimens previously attributed to either *finmarchicus* or *helgolandicus*.

Overall length measurement of each copepod was taken from the anterior tip of the cephalosome to the posterior tip of the caudal furcae (excluding the setae) using micrometer units equivalent to 0.027 mm. As will be seen from Table II,

TABLE II.

Sample No.		Number of specimens.	Size range in mm.	Mean size in mm.
I	<i>C. finmarchicus</i> .	179	2.77-3.85	3.27 ±0.015
	Doubtful .	5	3.28-3.49	3.39 ±0.042
	<i>C. helgolandicus</i> .	37	3.08-3.77	3.52 ±0.058
II	<i>C. finmarchicus</i> .	225	2.74-3.77	3.27 ±0.024
	Doubtful .	11	3.078-3.59	3.36 ±0.056
	<i>C. helgolandicus</i> .	94	3.18-3.80	3.58 ±0.014

there was almost complete overlap in the size ranges of the two forms, although their mean sizes were significantly different. Those individuals of doubtful affinity in terms of cephalosome profile also gave intermediate lengths, so confirming Rees' suggestion of a gradation of characteristics in a cline system.

The object of this short study was to investigate more closely the relationship between body length and the denticulations on the basal segment of the 5th leg in the females of the two forms. A number of workers have commented on the variation in the number of teeth and some have considered the possibility of it being related to the size the animal. For example, Mrazek (1902) found a wide size range, 3.4 mm. to 5.2 mm. in adult females in a single sample from Spitzbergen. He tried unsuccessfully to use the denticulation on the 5th legs as a diagnostic. Currie (1918) found a range of teeth varying from 24 to 42, but after arranging her animals in groups based on the number of teeth, she found wide ranges of body length in each category. Farran (1929) compared specimens taken off the south coast of Ireland with others collected around New Zealand and in the Antarctic. He found the latter to be smaller and to have only 17 or 18 teeth compared with 26 to 40 teeth in the former. Jespersen (1934) followed up this observation by counting the number of teeth in 20 individuals from each of two distinct size groups found in West Greenland samples. The largest size group with cephalosome lengths

ranging from 3.27 mm. to 4.15 mm. had 29 to 38 teeth, giving an average of 34.1, while the smaller, 2.11 to 2.92 mm., had 27 to 43 teeth with an average of 34.8. Reasonably, he concluded that in this sample the number of teeth was not a criterion of size. As it was not determined in any of these cases whether the copepods investigated were *C. finmarchicus* or *C. helgolandicus* or a mixture of the two, it was thought that something might be gained by repeating a comparison between body length and number of teeth in samples of known type, in the hope that some less subjective criteria of the differences between the two forms might so be revealed. No such diagnostics were found, but the results may be of value to other workers interested in the relative status of *C. finmarchicus* and *C. helgolandicus*.

The adult females from Samples III, IV, V and VI (Table I) were used. Sample III comprised a pure stock of *C. finmarchicus*, Samples V and VI only *C. helgolandicus* and Sample IV a mixture of the two. Lengths were taken in units of 0.027 mm. as before and the numbers of teeth on the basal joints of the 5th legs were counted. Occasionally it was found that one basipodite carried more teeth than the other, in which case the higher count was used. It soon became noticeable that there was far more often an even number of teeth on a leg than an odd number. Details of the measurements and counts are given in Table III.

TABLE III.

Sample No.	Number of specimens.	Size in mm.			Number of teeth.		
		Range.	Mean.		Range.	Mean.	
III . <i>C. finmarchicus</i>	168	2.72-3.85	3.19	± 0.012	24-51	37.30	± 0.41
IV . <i>C. finmarchicus</i>	490	2.75-3.82	3.35	± 0.008	24-65	41.61	± 0.27
<i>C. helgolandicus</i>	100	2.82-4.00	3.57	± 0.012	23-47	35.31	± 0.43
V . <i>C. helgolandicus</i>	161	2.97-3.80	3.42	± 0.013	27-51	36.34	± 0.29
VI . <i>C. helgolandicus</i>	251	2.82-3.90	3.46	± 0.013	24-45	35.17	± 0.29

It is immediately clear that the samples were taken from populations of very different size distributions. This was, of course, to be expected. Many workers, for example Rees (1949) and Wiborg (1954) have given size frequency curves showing wide ranges of characteristics despite the fact that they were derived from samples taken comparatively close together in space and time. Throughout the series the average size for *helgolandicus* was significantly larger than for *finmarchicus*, although there were also significant differences between samples of the same form. However, the mean size of *finmarchicus* varied by 0.26 mm. in four samples and that for *helgolandicus* by 0.16 mm. in five samples, while the difference between the largest mean value obtained for *finmarchicus* and the smallest for *helgolandicus* was only 0.07 mm. It seems, therefore, quite likely that a more comprehensive set of samples would reveal cases in which the mean size of *helgolandicus* was less than that of

finmarchicus; it is known that the size of these copepods varies with season. Although, as was to be expected, the smallest individuals in this series were *finmarchicus* and the largest *helgolandicus*, there was an overlap covering some 80% of the combined range.

It is equally plain from Table III that there is no consistency between samples in the frequency distribution of individuals of either form in terms of the numbers of teeth on the basipodite of the 5th leg. Here again the difference between the means found for either form is greater than that between selected samples of *finmarchicus* and *helgolandicus*; this, despite the fact that only two samples of the former and three of the latter were analysed. The overlap amounted to more than 50% of the combined range.

It would appear, therefore, most unlikely that any sound diagnostic can be based on either overall size alone or the number of teeth alone, although the shape of the teeth and their orientation on the basipodite may well provide an adequate characteristic.

The relationship, if any, between the length of individuals and the number of teeth on the 5th legs was next tested. The animals in each sample were arranged according to their number of teeth and the variance in body length *between* and *within* the arrays was computed. In Sample III the number of teeth ranged between 24 and 51, so that the 168 individuals were divided between 28 arrays, giving the following analysis of variance:

		d.f.		s. of s.		m.s.		v.r.	
Between arrays	.	27	.	2.0807	.	0.0771	.	4.4	P 0.001
Within arrays	.	141	.	2.4942	.	0.0177			
Total	.	168	.	4.5749					

There are, then, highly significant differences between the array means which can be considered to comprise two parts; one representing the linear regression of mean lengths on numbers of teeth and the other the deviations of the observed means from a straight line:

		d.f.		s. of s.		m.s.
Regression	.	1	.	0.8543	.	0.8543
Deviations from regression	.	26	.	1.2264	.	0.0472
Between arrays	.	27	.	2.0807		

The deviations from regression are clearly larger than would be expected if the regression of the means on the numbers of teeth was really linear since the variance ratio, $0.0472/0.0177 = 2.7$, is highly significant.

A similar analysis of the *C. finmarchicus* from Sample IV also gave significant differences between array means, and a highly significant divergence from a straight line relationship between body length and number of teeth.

Two samples of *C. helgolandicus* (V and VI) treated in the same manner revealed no significant differences between the mean sizes of individuals carrying various numbers of teeth or any linear relationship between mean length and number of teeth.

The possibility of differentiating between individual specimens of *finmarchicus* and *helgolandicus* on the basis of their body length and number of teeth was also examined. The following linear discriminant function was derived for the purpose :

$$y = 0.0748t - 2.1685l$$

in which t = number of teeth and l = body length of any individual. The mean values of $\bar{y}$ for *finmarchicus* and *helgolandicus* were found to be -4.1162 and -4.8549 respectively. The difference 0.7387 , has a small standard error of 0.0355 and is significant. However, it was found that the probability of misclassifying an individual on this basis would be as high as 27%. Such a discriminant function is, therefore, ineffective.

This work was done while I was a student assistant under Dr. J. H. Fraser at the Scottish Home Department Laboratory, Aberdeen. I am indebted to him for suggesting the problem and for his encouragement. I should also thank Dr. C. E. Lucas and Professor C. M. Yonge, for their helpful criticism, and Dr. S. D. Silvey and Mr. J. H. Pope for their guidance in the statistical analyses.

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AN ECOLOGICAL SURVEY OF THE DRIFT-NET HERRING FISHERY OFF THE NORTH-EAST COAST OF SCOTLAND

PART I:

ON SAMPLING BY THE COMMERCIAL FISHING FLEET.

BY

R. S. GLOVER, B.Sc., G. A. COOPER AND W. W. BROWN, B.Sc.

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AUTHORS' NOTE.

THIS work was started in 1947 in the Department of Oceanography, University College, Hull, through the encouragement of Professor A. C. Hardy. The survey was continued when, in 1950, the staff was transferred to the Edinburgh laboratory of the Scottish Marine Biological Association. Dr. G. T. D. Henderson initiated the survey in 1947 and was in charge for the first three years. Mr. A. Saville¹ and Mr. H. R. Schurr both helped considerably in the work before resigning their appointments to take up work elsewhere.

The authors wish to record their indebtedness to these colleagues and to

¹ Now on the staff of the Aberdeen Marine Laboratory of the Scottish Home Department.

Dr. C. E. Lucas¹ who all at various times participated in the internal work of the team.

The success of the survey was entirely dependent on the co-operation of the fishermen; it is impossible to praise too highly the assistance we have had from the skippers and crews of the herring drifters. Invariably they have provided the information which was required and have always been willing to discuss the mutual problems of fisherman and scientist, and to recount their own experiences and fishing lore. In addition, more than a hundred skippers have provided samples with the Plankton Indicator in the course of the survey; without this assistance the work could never have been carried out.

We are particularly grateful to the Scottish Home Department for making the landing statistics available to us immediately they were collected in the ports of Fraserburgh and Peterhead; we have gained considerable benefit from the advice and co-operation of Mr. B. B. Parrish of the Department's Marine Laboratory in Aberdeen.

INTRODUCTION.

Professor A. C. Hardy's study of the herring in relation to its animate environment (Hardy, 1924, 1926) led to a survey in the Scottish, Northumbrian and East Anglian drift-net fisheries (Hardy, Lucas, Henderson and Fraser, 1936). During this survey the Hardy standard Plankton Indicator was used by fishermen to obtain a sample of the plankton immediately before the drift-nets were shot; the catch of herrings was then related to the quantity and type of plankton in the immediate vicinity of each vessel.

This work was re-commenced in 1947 when the drift-net fishery from Fraserburgh, on the north-east coast of Scotland, was selected for an intensive study of the ecology of the herring. The number of plankton samples was limited by the number of drifter skippers who volunteered to use the Plankton Indicator, but the only limitation of information about herring catches was the size and distribution of the fishing fleet. During 1948 we began to collect details of the position and size of catches of herrings when they were later sold in the Fraserburgh market. This provided information about both the dispersal of fishing effort and the distribution of herrings, but it had the disadvantage that the small and "nil" catches, which did not appear in the market sales, were not included. This weakness was remedied when, in 1951, a detailed survey of all the north-east Scottish fisheries was started by the Aberdeen laboratory of the Scottish Home Department. The Statistics Collectors employed by the Department, under their Fishery Officers, were able to record the catches of *all* boats fishing in the area, irrespective of the port of landing, whether their catches were sold in the market or not. The summarized results of the first three years of this intensive collection have been presented in the 'Annales Biologiques' (Wood, Parrish,

¹ Head of the Department of Oceanography, University College of Hull, until 1948; now Director of Fisheries Research in the Scottish Home Department.

Baxter and McPherson, 1952, and Parrish, Baxter, McPherson and Buchan, 1953 and 1954).

As part of the study of the relationship between the plankton and the herring, samples of the fish have been obtained from the drift-net boats, for an analysis of stomach contents. Similar samples were used by the Aberdeen laboratory for biometric and biochemical analysis.¹

Samples of both plankton and herrings and, through the commercial catches, a measure of the abundance and distribution of herrings were, therefore, obtained directly from the fishermen. Normally, in ecological research the sampling methods are determined before an investigation begins; in the present survey they were, largely, the techniques of commercial fishing. The extent of the distribution and migrations of herrings make it essential to take samples from the widest possible area if one is to attempt to understand the causes of fluctuations in the commercial fisheries. Furthermore, previous work has not defined the problem sufficiently well to reduce the necessary range of techniques; investigations along many different lines of approach are desirable, probably over a long period of time.

Such an ambitious programme and sufficiently widespread sampling can, perhaps, only be achieved with the assistance of the commercial fishing fleets. However, as Gulland (1955) has said, the commercial landings are obtained by sampling in a far from random manner. One must therefore ask two questions. Firstly, to what extent does the non-random distribution of samples limit or bias information about the environment of the herring? Secondly, how far does the information about the catches reflect the distribution and total population of fish?

The account which follows discusses some of the characteristics and limitations of sampling from drift-net vessels and describes some features of the Scottish summer fishery during the period of the investigation. Parrish and McPherson (1956) have discussed some of the problems of sampling the herrings; they suggest that selection of fish by the meshes of the drift-nets does not appear to be a serious source of bias in the Scottish summer fishery.

The object here is to set the background for subsequent papers on the relation between the catch and the animate environment, on the plankton of the fishing grounds and on the feeding habits of the fish.

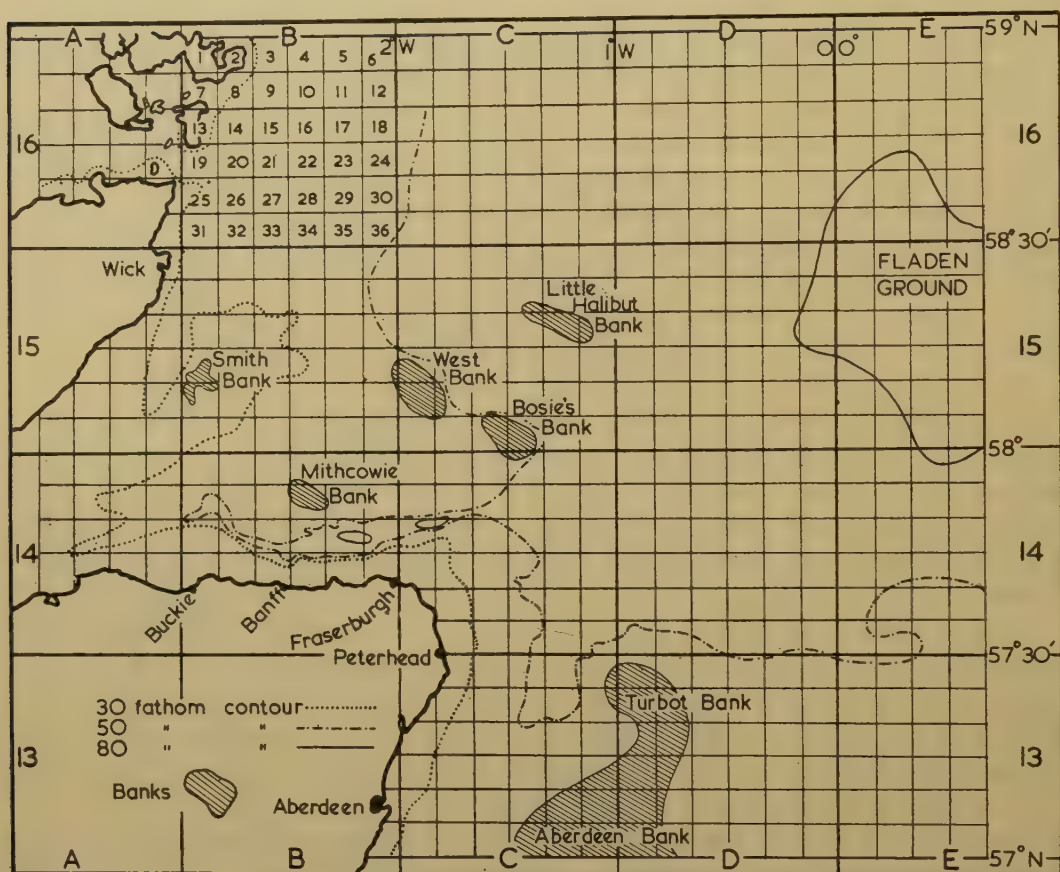
THE DISTRIBUTION OF FISHING.

The drift-net vessels fish only by night during the Scottish summer season and they usually return to port to land their fish during the following morning. There is no fishing on Saturday and Sunday nights, so that the working week consists of five nights' fishing, followed by a break of two days before the search for fish is resumed. Since the nets are shot only once in the course of a night's fishing, the expression "catch per shot" implies the catch per vessel per night.

¹ Most of the material for the present paper was collected between 1947 and 1952, but, because the work is a long-term study which is still proceeding, it has been possible to include some material from 1953 and, occasionally, from 1954.

The number of drift-nets used by each vessel varied, but was seldom less than 60 or greater than 80 nets. Except where it is otherwise stated the catches have been corrected to the theoretical catch in crans per 70 nets.

For convenience in charting and for the presentation of the material, the area has been divided into rectangles measuring five minutes of latitude by ten



TEXT-FIG. 1.—The area from which most of the samples were taken. The small squares, described in the text as “five-mile squares” measure five minutes of latitude by ten minutes of longitude and are sub-divisions of the standard International squares indicated by the letters and numbers at the edges of the chart. A system of reference to the “five-mile squares” is shown in International square B 16.

minutes of longitude. The rectangles, which approximate to squares with an area of 25 square miles, are shown in Text-fig. 1; they are based on the standard International system and are referred to in the text as “five-mile squares”.

Differences between years.

Text-fig. 2a shows the area which was fished in each of the six years from 1947 to 1952. The most heavily fished grounds lay in the sector between north

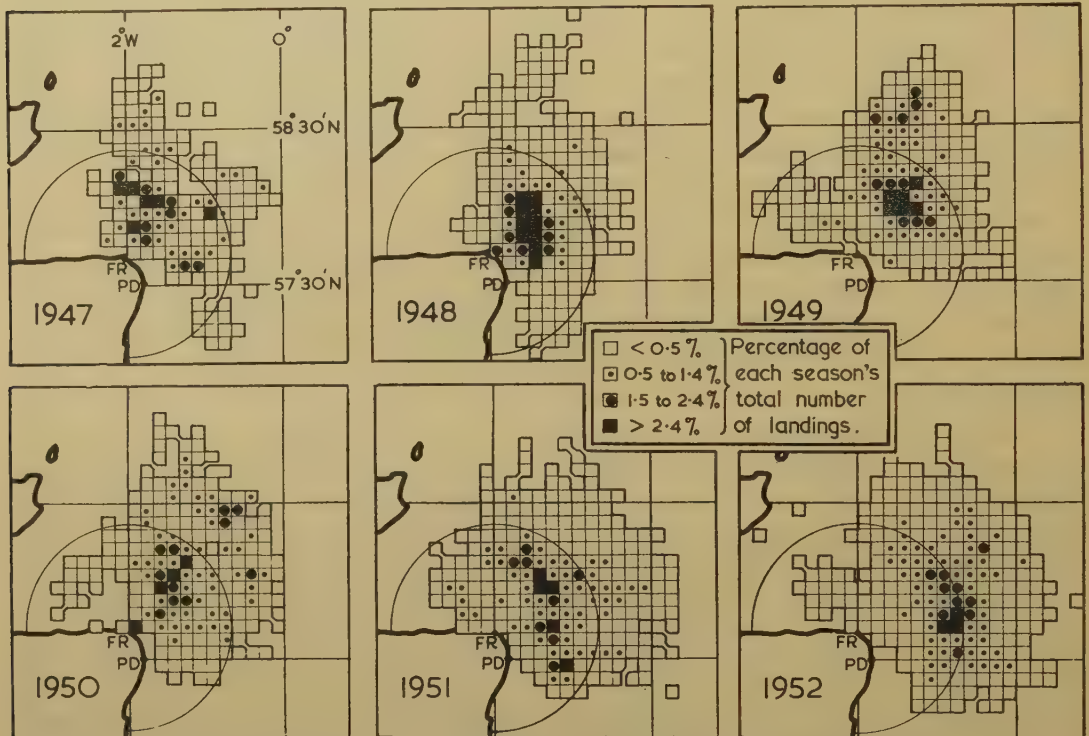
and east of Fraserburgh and were generally about 20 to 30 miles offshore except in 1952 when the greatest fishing effort was about 40 miles or more from port. About twice as many shots were obtained beyond the 40-mile range in 1952 as in any of the previous five years.

Whilst, with the exception of 1952, the area of intensive fishing lay inside the 40-mile radius, that of high average catch lay outside this radius in all the years of the survey. This is shown in Text-fig. 2*b*, where the mean catch per shot is shown in each five-mile square. There was in every season a distant and fairly well-defined area of high catches. A similar distribution may be seen in a paper by Wood and McGee (1925), who surveyed the fishing grounds from the air in July, 1924. From their charts II-V it is apparent that the best catches were most consistently taken some 50 to 70 miles from Fraserburgh; indeed, the most productive fishing occurred in precisely those areas yielding catches of more than 25 crans per shot in 1947-49. During the period 1947 to 1951 this more distant and more productive area was visited spasmodically by small numbers of boats, but in 1952 it was regularly fished by many vessels. Text-fig. 2*b* shows on the whole a gradient of increasing yield with increasing distance from port; in 1952 alone there was an indication of a declining gradient of catches at the outermost edge of the fished area.

The major concentrations of fish appeared to lie to seaward of the intensively exploited area and perhaps even further east, outside the radius of Scottish fishing. Certainly the evidence of Wood and McGee (1925), quoted above, and the Dutch fishing results, quoted below, support the suggestion of an offshore region of high productivity. In 1952 the average catches in the waters beyond the 40-mile range were higher than previously, but fishermen made more frequent visits to this area than in the earlier years. The increased searching efficiency of a large number of boats might be expected to raise the average catch even if there were no increase in the stock. From echo-sounding and stock-analysis, however, there are reasons for believing that the stock may have been greater in 1952 than previously, but it must be pointed out that in former years there was less economic stimulus to steam long distances; fish landed late in the day were generally sold for conversion to meal and oil at about half the price of fresh fish landed earlier. However, during the early part of the 1952 season there was only a small demand for fresh fish, so that most of the landings were being used for conversion to meal and oil, the price of which had risen by over 40% during the previous two years. Economic factors should therefore be considered together with biological factors in any attempt to assess the distribution of herring during the 1952 fishery.¹

¹ As an instance of the kind of factor which may be decisive, it should be mentioned that a chance shot on the distant grounds to the south-east of Fraserburgh was reported by a vessel returning to port in mid-April of 1952, before the expected commencement of the normal summer season. One of the authors met skippers discussing this high catch which had occurred in an unexpected locality; in consequence of this news the fishermen hurriedly prepared to go to sea to exploit that area rather than fish the more normal grounds to the north and west of Fraserburgh.

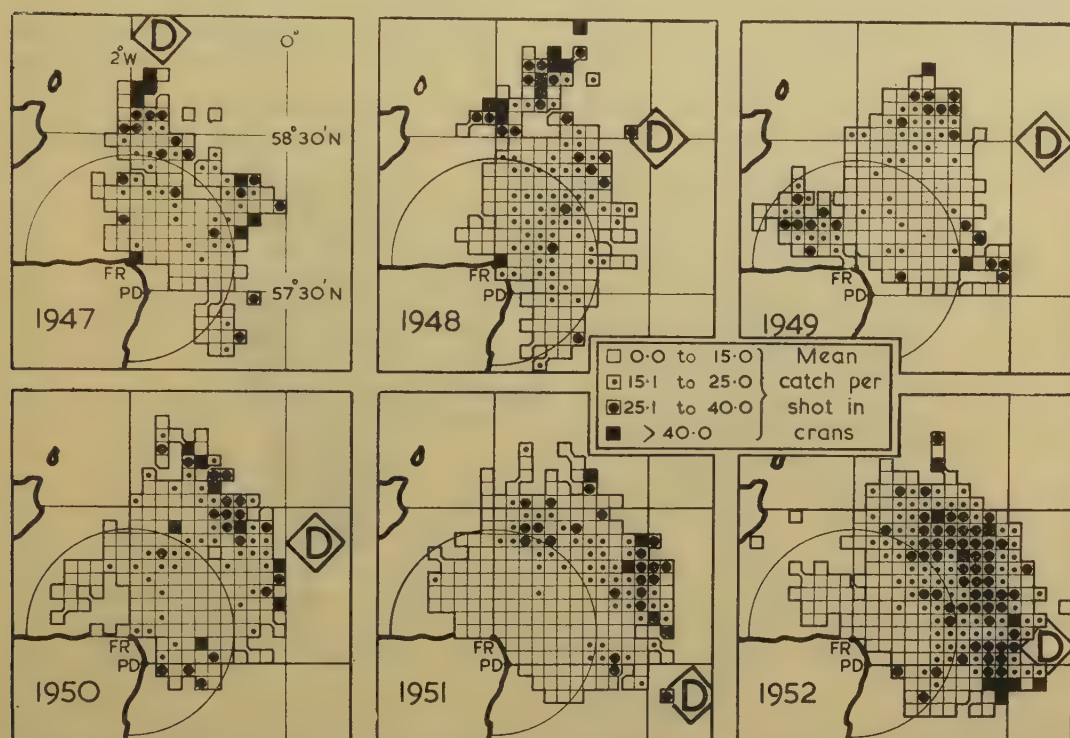
Wood and McGee (1925) showed that the highest catches in July, 1924, were most often taken north of lat. $58^{\circ} 20' \text{ N}$. A similar distribution was found from 1947 to 1949, when an area of relatively high catches was found north of $58^{\circ} 30' \text{ N}$. (Text-fig. 2b); during those years this productive region may have shifted progressively eastwards. Subsequently, the eastwards trend continued on a less marked scale, but there was a pronounced southerly shift.



TEXT-FIG. 2a.—Charts showing the distribution of fishing effort during each season. The circle is drawn at a radius of 40 miles from Fraserburgh. The source of the material varied in different years (see text, p. 142). Catches landed at Fraserburgh alone were used from 1947 to 1950; in 1951 and 1952 landings at Fraserburgh (FR) and Peterhead (PD) were used.

A similar south-easterly shift can be seen in the published results of drift-net fishing by Dutch vessels (De Veen and Boerema, 1949; De Veen, 1949, 1950, 1951, 1952, 1953 and 1954). The area fished by Dutch drifters is illustrated by these authors in charts, one for each month, showing the catch per shot. The July charts alone provide a complete picture, through the years, of Dutch fishing in the Scottish area. The locality of the most productive fishing by Dutch vessels in July of each year has, therefore, been super-imposed on Text-fig. 2b. The positions have been selected by eye, but they are probably an adequate estimate of the most productive localities as the areas of high catches are clearly defined and localized in the pub-

lished figures. There is a very close agreement between the southwards shift of the best fishing from 1947 to 1952 in both the Scottish and the Dutch statistics. It is notable that the Dutch vessels always took their best catches a little to seaward of the Scottish boats; coupled with the gradient of increasing Scottish catches with distance from port, this provides further evidence that the greatest abundance of herrings may have occurred outside the area normally fished by Scottish boats.



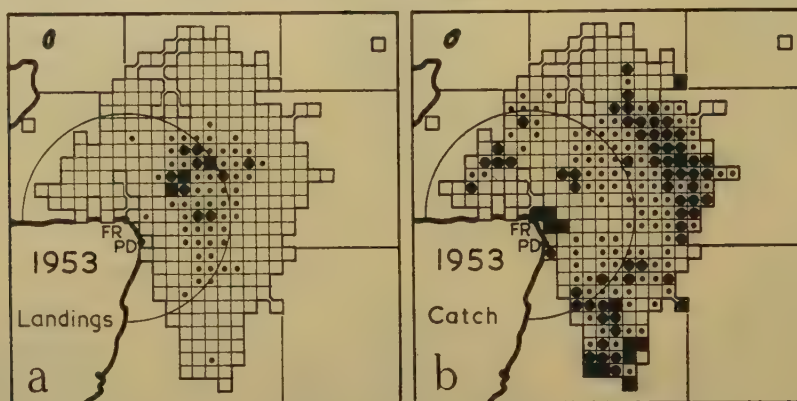
TEXT-FIG. 2b.—Charts showing the mean catch of herrings from each of the five-mile squares during each season. See legend for Text-fig. 2a for comments on the source of the material. The symbols represent the mean catch in crans per shot, expressed as crans per 70 nets. The position of the highest mean catch taken by Dutch drifters in July of each year is shown by a "D" inside a diamond (see text, p. 146).

Text-fig. 3 shows the distribution of (a) Scottish boats and (b) their catches in 1953. Whilst the majority of the boats continued to fish about the 40-mile radius, there was a considerable southerly extension of the fishing and the best catches were found, in 1953, about 30 miles south of the most profitable locality of the previous year. The best Dutch fishing, in July, was about 60 miles to the south of the area illustrated in Text-fig. 3 (De Veen, 1954).

Both the Scottish and Dutch results show a southerly extension of the area fished, as distinct from that which yielded the best catches. This is clear from Text-fig. 4, which shows the distribution of average catch along a track 10 miles

wide running due south from $58^{\circ} 45' \text{ N.}$ This 10-mile track, from $0^{\circ} 50' \text{ W.}$ to $1^{\circ} 10' \text{ W.}$ (*i.e.* centred about the meridian of 1° W.) was chosen because it was fairly well sampled throughout the investigation, and, being clear of the land, it was free of the peculiarities of the inshore fishing for spawning herrings.¹

The first two years have been omitted from Text-fig. 4 because during 1947 and half of the 1948 season only limited information was available (see p. 142); during these two years the best fishing was to the north of $58^{\circ} 30' \text{ N.}$ and a little to the east of the selected 10-mile track. In 1949, 1950 and 1951, the highest mean catches were again found to the north of $58^{\circ} 30' \text{ N.}$ and there was a declining gradient to the south; during these three years there was a progressive southerly extension of the region producing catches above the average. In 1952 and 1953



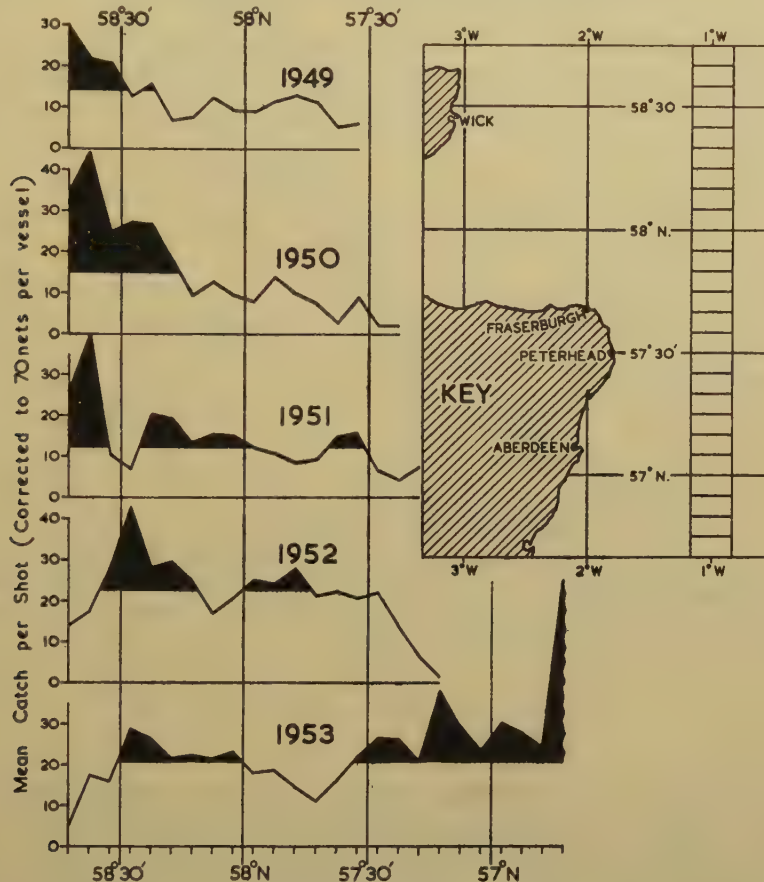
TEXT-FIG. 3.—Charts for 1953 showing (a) the distribution of fishing effort and (b) the mean catch per shot in five-milesquares. For further details and keys, see legends for Text-figs. 2a and 2b. All catches landed at Fraserburgh (FR) and Peterhead (PD) have been included.

the catches north of $58^{\circ} 30' \text{ N.}$ were below average and in the latter year the best fishing was found at the southernmost end of the track. The southerly limit of high catches has not only extended southwards, but the northerly limit has retreated from the north. This progressive southerly shift of the area of most productive fishing was evidently independent of the parallel shift of fishing effort, which was, indeed, slight prior to 1953.

This apparent southerly shift of the herring population may not have been restricted to the Fraserburgh and Peterhead grounds. Text-fig. 5 shows, in tabular form, the average catch per shot in each year at Lerwick in Shetland, to the north of the area investigated here, and at Fraserburgh and Peterhead, the figures being calculated from the Fishery Officers' reports. It is clear that in 1947 and 1948

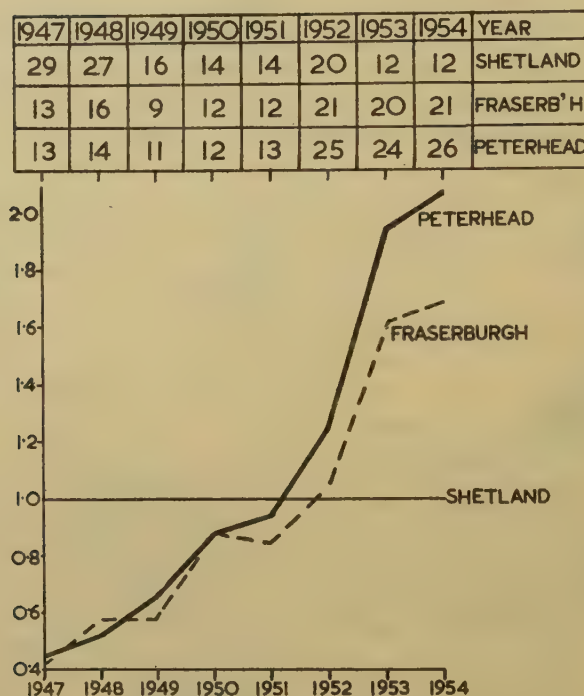
¹ During August, when spawning occurs, the manner of shoaling of the fish is probably different from that which obtains during the rest of the year; very large catches are often taken from inshore positions over a period of a few days when spawning is imminent. The risk of losing nets through an overweight of fish has discouraged the fishermen from fishing in the spawning concentrations in some of the years of the investigation.

the best average catch came from the Lerwick grounds in the north, and in 1952, 1953 and 1954 from Peterhead in the south. If the Fraserburgh and Peterhead catches are expressed as a proportion of the Lerwick catches (graph in Text-fig. 5) it is at once obvious that the catches at the southerly ports have increased, progressively and uniformly relative to the catches at Lerwick.



TEXT-FIG. 4.—The mean catch of herrings in crans per shot plotted along a north-south track, ten miles wide, centred about the meridian of 1° W. (see inset key). Each point on the graph represents the mean catch inside a rectangle formed by the fusion of two adjacent five-mile squares. The blacked-in part of the graphs indicates values greater than the annual mean catch by *all* the boats whose positions and catches were recorded at the ports.

There appears, therefore, to have been a progressive re-distribution of the available stock of herrings; more knowledge of the composition of the catches is required before one can say whether this re-distribution resulted from a southerly migration of the fish or from fluctuations in the stocks on each of the fishing grounds. This investigation of the stock composition is being undertaken in the Aberdeen laboratory of the Scottish Home Department.



TEXT-FIG. 5.—Table (above) showing, in each year the average catch of herrings in crans per shot by vessels fishing from the Shetlands, from Fraserburgh and from Peterhead. Graphs (below) showing the average catch, in each year at Fraserburgh and Peterhead, expressed as a proportion of the catch at Shetland.

Differences within years.

The fishing fleet did not fish the same locality consistently throughout each season; within each year there were both gradual and abrupt shifts of ground. This is clear from Text-fig. 6 which shows, day by day during 1950 and 1953, the percentage of the catches landed at Fraserburgh which were taken more than 40 miles from that port, *i.e.* outside the circle shown in Text-figs. 2 and 3. At the beginning of the season many boats fished inside the 40-mile radius; in mid-season almost every vessel was fishing more than 40 miles from port; and then this was followed by a most abrupt change in July from offshore to wholly inshore fishing. With the exception of 1952, a similar sequence was found in all the years of the survey. Each season has been divided into three phases, according to the area which was fished; Table I shows, during each of these phases, the percentage of the Fraserburgh vessels which fished outside the circle at 40 miles.

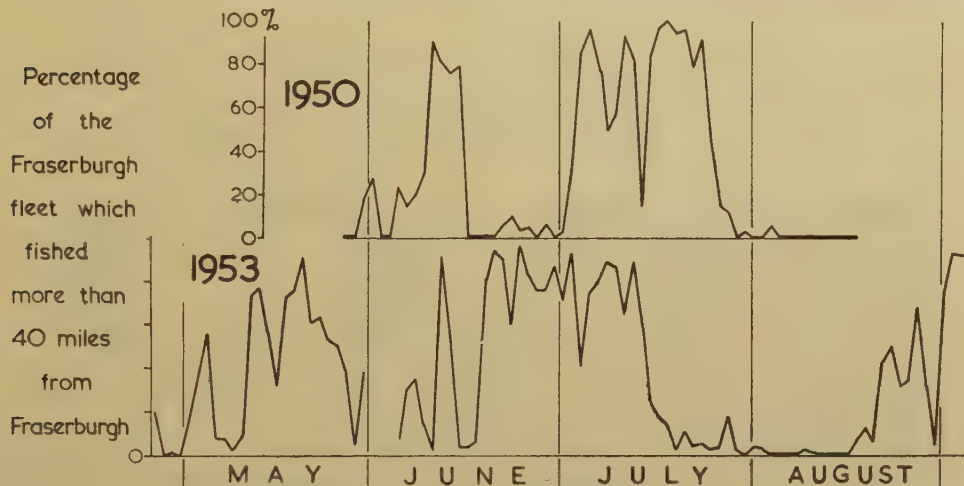
Atypical results were obtained in the early periods of 1949 and 1952. In 1949 this may have resulted from a restriction imposed by the fishermen on the area to be fished. The unusual character of 1952 has already been discussed;

TABLE I.—*Percentage of the Catches Landed at Fraserburgh which were Obtained by by Vessels Fishing more than 40 miles from Fraserburgh.*

For dates, see Text-fig. 7.	1947.	1948.	1949.	1950.	1951.	1952.	1953.
Early period . . .	No data .	15.2 .	1.0 .	33.1 .	8.1 .	75.9 .	29.0
Mid-period . . .	34.8 .	48.2 .	38.7 .	51.7 .	37.7 .	59.9 .	56.1
Late period . . .	3.7 .	0.6 .	No data .	0.8 .	7.2 .	11.8 .	7.6

it is apparent that the increased amount of fishing in distant waters in that year occurred during the early part of the season.

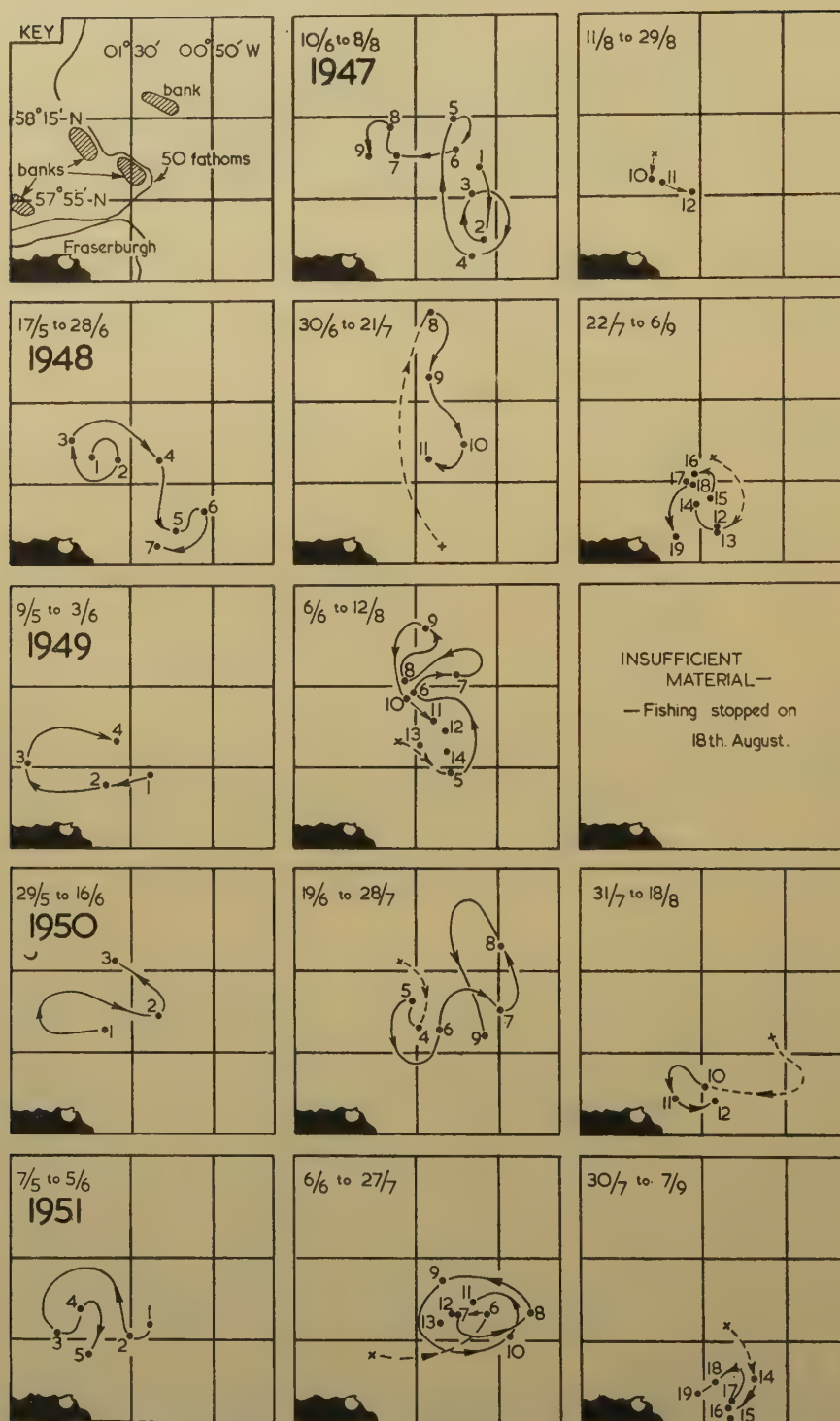
The basis of the present division of each season into three periods or phases



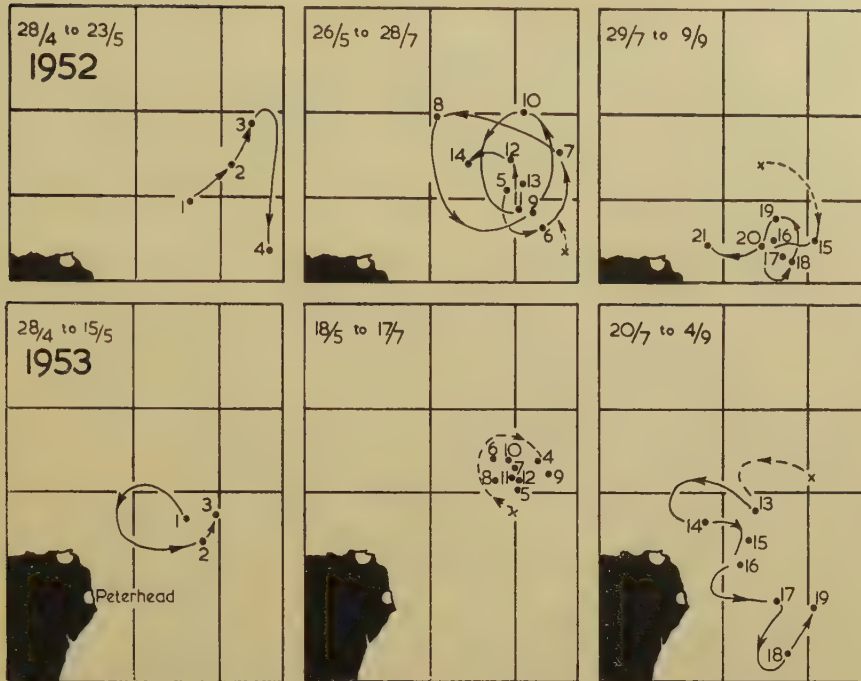
TEXT-FIG. 6.—Graphs showing, day by day, the percentage of catches landed at Fraserburgh which were obtained more than 40 miles from that port. The break in the graph in early June, 1953, resulted from the short holiday with which the fishermen celebrated the coronation of the Queen.

is illustrated in Text-fig. 7 which shows the “geometric centre” of the fishing fleet during each week of seven summer seasons. The centre of fishing effort was found by plotting the number of vessels fishing in each five-mile square in each week. The numbers were then summed in five-mile columns of longitude and in five-mile rows of latitude. From these totals the “mean fishing position” could be calculated along the east-west axis and along the north-south axis; *i.e.* the average fishing position was expressed as the distance eastwards from a datum (3° W.) and as the distance north from another datum (57° N.). The intersection of the two positions gave a point which represented the centre of fishing effort. The arrows which connect the successive centres in Text-fig. 7 provide a general impression of the route of the fleet over the sea, as seen from the day-to-day distribution of fishing vessels.

The comparison just made of fishing results in different years would seem to suggest a pattern of biological significance. It is now apparent that there was



TEXT-FIG. 7.—See legend opposite.



TEXT-FIG. 7.—Charts showing the geometric centres of the fishing fleet, week by week, during 1947 to 1951 (on the left) and 1952 and 1953 (above). The centres are numbered 1, 2 . . . etc., to indicate the first, second and succeeding weeks, starting at the beginning of each season except 1947 when the survey began one month after the commencement of fishing. The arrows show the approximate path taken by the fleet over the sea. Each season has been divided into an early, middle and late phase, according to the locality which was fished (see text, pp. 153, 154); the dates of each period are shown in the top left-hand corner of each chart.

also a pattern within each season; the fleet, in exploiting the herring, pursued a similar course over the area during each year. This pattern is conveniently displayed in the form of a three-phase season although the dates at which the divisions have been made might be changed without obscuring the general picture of movement over the sea. Wood, in his Buckland lectures of 1932, divided the season into three phases on the basis of yield and he also (Wood, 1930) referred to the movements of the fishing vessels, particularly towards the end of the season when the inshore spawning fishery occurs.

The three phases of the fishing season which are illustrated in Text-fig. 7 may be defined as:

1. *Early period.* During April, May and early June, there was fishing to the west of $1^{\circ} 30' W.$ and sometimes to the south of $57^{\circ} 55' N.$ (see key in Text-fig. 7), mostly over water of less than 50 fathoms depth. This may be described as the western banks fishery, for the fishermen frequent Mith-

cowie, West and Bosie's Banks which serve as navigational aids and are traditionally associated with high catches.

2. *Middle period.* During late June and most of July, the fleet was found in the central and eastern part of the region, with occasional excursions to the north, that is, fishing mostly to the east of $1^{\circ} 30' W.$ and north of $57^{\circ} 55' N.$ These are deep water areas with more than 50 fathoms of water under the drift-nets.

3. *Late period.* Towards the end of July the fleet moved to the south of latitude $57^{\circ} 55' N.$ and subsequently shifted, week by week, westwards and shorewards until the end of the season found most of the boats within the area limited by the coast-line and by $57^{\circ} 55' N.$ and $1^{\circ} 30' W.$

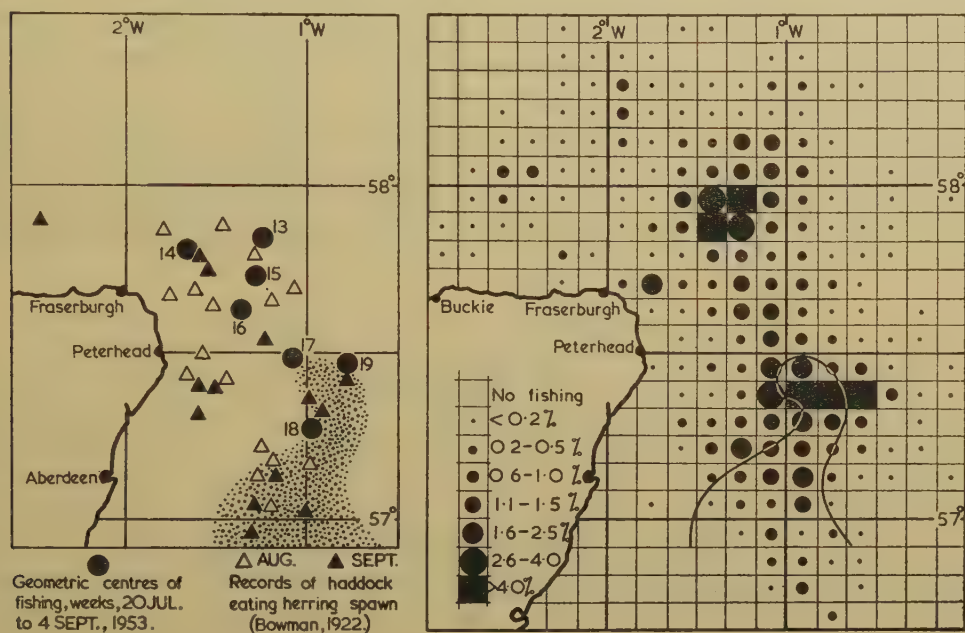
There were some variations of this typical pattern. For instance, in 1947, the southerly movement towards the spawning grounds took place to the west of the mid-season grounds instead of by the more usual easterly route. The most striking variations were found in 1952 and 1953 when there was no early fishing on the westerly banks. A long-term southerly shift of herrings has been suggested above; it may be that results in 1952 and 1953 reflect this southwards shift. Indeed, the three phases of 1953 stand in the same spatial relation to each other as in the preceding years; the first phase was the most westerly, the second to the north-east of the first, and the final phase well to the south of the other two. But the whole annual effort has, so to speak, shifted southwards round the projecting coast of Aberdeenshire.

A final assessment of the significance of these three phases of fishing must await the completion of the Aberdeen laboratory's study of the stock composition. However, a preliminary inspection of the age and maturity analyses of fish used for stomach-content analysis and of the interim results published in the 'Annales Biologiques' (Wood *et al.*, 1952, and Parrish *et al.*, 1953 and 1954) suggest at least a rough correspondence between the three phases of fishing effort and the stock composition. During the early part of the season, immature and recovering spents from all age groups were taken; during mid-season the fish were mostly young and maturing, whereas, towards the end, older fish returned to the shoals when feeding was slight and most of the fish were sexually mature. It seems possible, therefore, that the pattern of fishing described here may reflect the pattern of migration of different components of the stock of herrings. Migration was, perhaps, most clearly suggested by the shift of fishing effort during the final six to eight weeks of each fishing season. Whereas there were no consistent migratory patterns within the first and second phases of each year, the final period of each year was characterized by movement shorewards towards the spawning grounds.

In 1953, however, after a short south-westwards shift, the fleet moved to the south-east and fished further south than in the previous years.¹ It is possible

¹ The results for 1954 which appeared after this paper was written, show that the boats fished even further south during the spawning fishery than they did in 1953.

that, as a corollary to the southwards shift of the herring stock, spawning in 1953 extended further south than in the preceding six years. The Turbot Bank (see Text-fig. 1) was specified by Wood (1930) as an autumn spawning ground; in the Reports on the Fisheries of Scotland it is stated that the concentration of spawning fish over Turbot Bank in 1953 was the most remarkable for many years and that there was little spawning over the Moray Firth Banks (Lucas, 1954 and 1955). The precise identification of spawning sites is not easy; Bowman (1922) used reports by trawler skippers, of "spawny haddocks", that is haddocks whose stomachs contained herring eggs. In Text-fig. 8 (left), localities which Bowman presumed



TEXT-FIG. 8.—(Left)—Chart, taken from Text-fig. 7, showing the geometric centres of fishing during the late phase of 1953. The herring spawning grounds shown by Bowman (1922) have been superimposed. The Turbot and Aberdeen banks (see Text-fig. 1) are indicated by the dotted area.

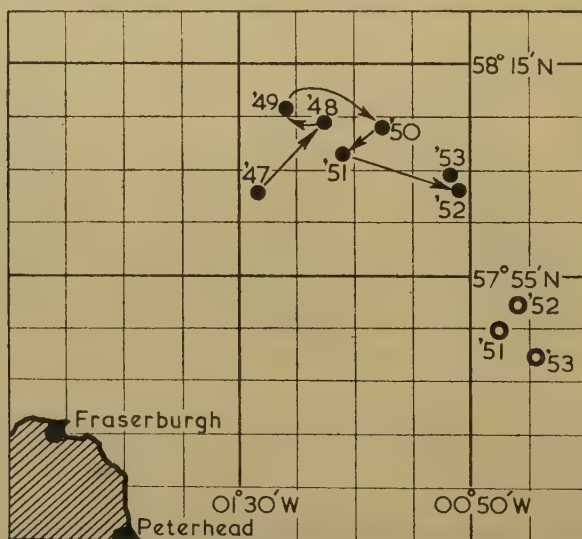
(Right)—The distribution of fishing boats during the same period, expressed, in each five-mile square, as the percentage of the total number of shots landed at Fraserburgh and Peterhead. The symbols represent the mean of the percentage distributions during each of the seven weeks.

to be herring spawning grounds are shown, together with the week-by-week centres of fishing during the third phase of 1953. Because the geometric centres do not necessarily indicate regions of aggregation of fishing vessels, the distribution of fishing effort during the same period is shown in Text-fig. 8 (right).

It appears from the weekly centres that the fishing fleet visited the spawning grounds in turn, beginning with the northerly spawning sites in early August and

finishing on the Turbot Bank in early September. It is further apparent from the distribution of fishing effort, that there was more fishing on the offshore spawning grounds than inshore and that the heaviest effort was directed towards the Turbot Bank. The two areas of concentrated effort do not reflect fishing from the two ports; the northerly patch represents concentrated effort during late July and early August whilst the Turbot Bank patch resulted from fishing in late August and early September.

It should be remembered that the results illustrated in Text-fig. 7 refer to Fraserburgh only during 1947–1950, but that in 1951, 1952 and 1953 statistics were obtained from the combined Fraserburgh and Peterhead fleets. It is clear, however, that the changed picture in 1952 and 1953 did not result from the addition of the Peterhead catches; as Table I shows, the Fraserburgh vessels were also affected by the tendency to fish further from port. Furthermore, the course of fishing shown in Text-fig. 7 for 1951, which refers to both ports, closely resembled that found for Fraserburgh alone in previous years. Although the fleets from the two ports intermixed, there is no doubt that the Peterhead vessels tended to fish a little to the south of the Fraserburgh boats. The nature of the different fishing



TEXT-FIG. 9.—Chart showing the geometric centres of the fishing fleet during the middle period of each annual season from 1947 to 1953; the dates of the middle period are shown in Text-fig. 7. The centres of the Fraserburgh fleet are shown by black dots, and those of the Peterhead fleet, during the three years for which information is available, by open circles.

practices at the two ports is illustrated in Text-fig. 9, which shows the geometric centres of the Fraserburgh and Peterhead fleets during the middle period of each season. Analysis of the first and last periods is limited by the late start of the survey in 1947, the early end of the 1949 season, an industrial dispute in May 1950, and by the varying number of vessels in every year when fishermen joined

or left the local fleet as each season started or drew to its close. During the middle period of each year the numbers of vessels were fairly stable.

Two points emerge from Text-fig. 9; firstly, there was a consistent difference between the positions of the Fraserburgh and Peterhead fleets. This reflected the different location of the two towns; during the three years for which information was available the geometric centre of each fleet was about E.N.E., 40 to 45 miles from each home port. Secondly, whilst the locality fished by Peterhead vessels remained most constant, the Fraserburgh fleet shifted eastwards between 1951 and 1952. Indeed, the centres for the seven years show a progressive eastwards movement; in 1947 the centre of the Fraserburgh fleet was less than 30 miles from port, compared with nearly 45 miles in 1953. A southward movement of fish, from the areas of maximum abundance in the early part of the survey, must result in an eastward shift in order to avoid the land. On the assumption that the fleet follows the herrings, therefore, the shift of Fraserburgh vessels towards the Peterhead grounds may reflect a progressive shift of the herring population towards the normal Peterhead fishery, resulting in the increasing success of boats from that port relative to their neighbours in the north (see Text-fig. 5)

THE MECHANISM OF FLEET SEARCHING.

The sampling ideal of a random distribution of vessels is never likely to be achieved in a commercial fishery. Fishing boats tend to aggregate in one or more localities, and the positions of such aggregations are likely to change from day to day. The object here is to discover if the samples obtained from fishing vessels are adequate for an ecological survey. But trends and patterns of fishing practice and results have been used above to infer biological phenomena and, in particular, to suggest migrations of herrings. This process of reasoning is dependent on the assumption that fishermen search the sea sufficiently to discover and keep in contact with the shoals of herrings.

In their search for herrings, fishermen are influenced by factors of two types. Firstly there are what might be described as transient factors—information about the location and success of contemporary fishing, indications of herring shoals on the echo-sounder, the sight of gannets and other birds diving into shoals of fish, and the opacity and colour of the water. Secondly there is a permanent factor—the belief, compounded from the individual fishermen's experience and from tradition, that herrings are likely to be abundant in certain localities and at certain times of the year.

The resultant of the factors influencing the fishermen in their choice of ground is shown in the seasonal pattern of fleet movement which was demonstrated in the previous section. What part is played by individual catches and by fleet-searching in the synthesis of this pattern?

Text-fig. 10 shows the distribution of fishing vessels and the size of their catches during twelve successive nights' fishing in 1950, when information was

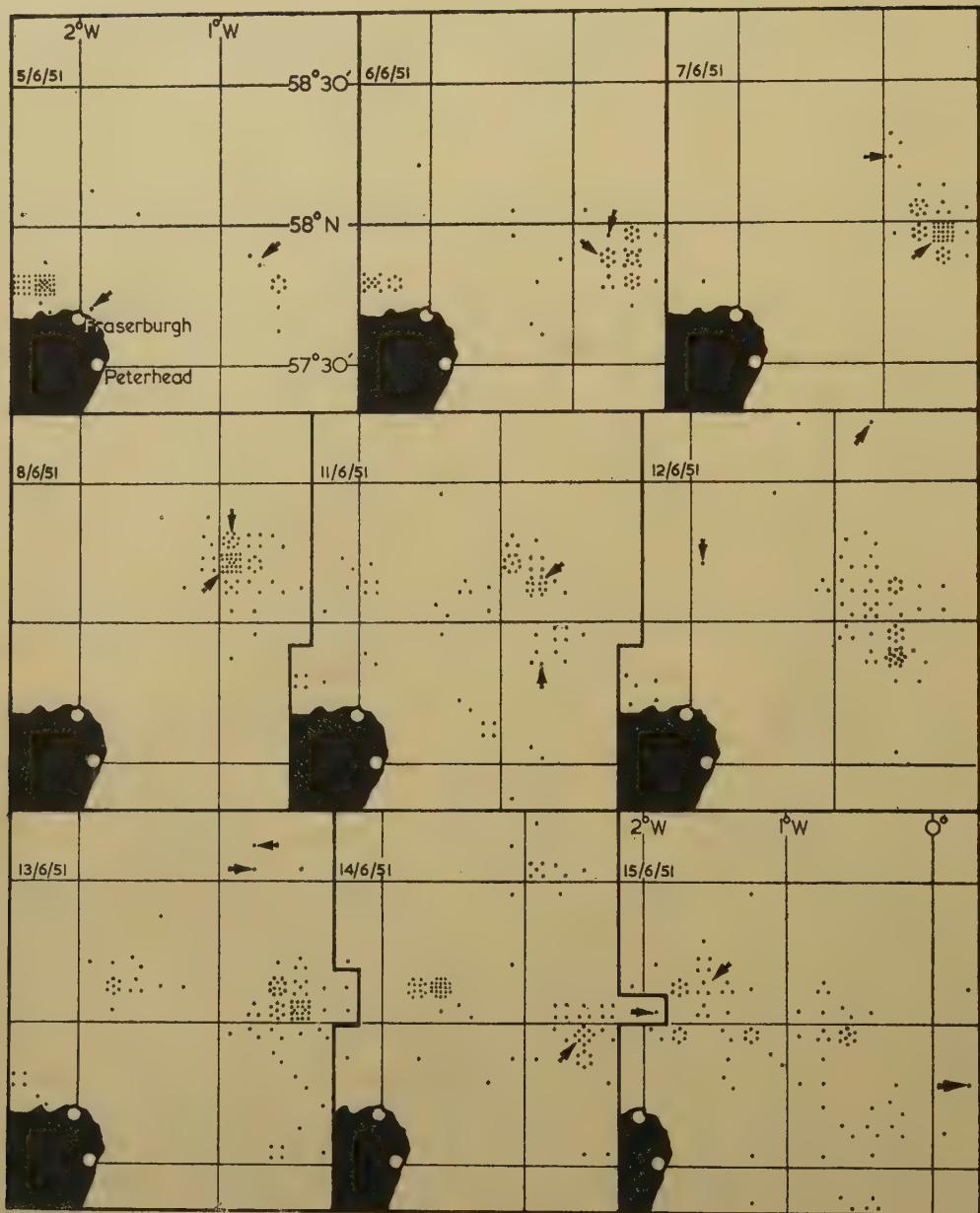


TEXT-FIG. 10.—Charts showing the distribution of fishing vessels and the size of their catches during twelve successive nights' fishing in 1950. The material relates only to catches recorded at Fraserburgh and represents about half the total fleet at that port. The arrows indicate the two highest catches in each night,

available from about half the total fishing fleet (see p. 142). The boats were scattered and the catches were low on the first day when the two best shots came from a boat in the centre of the fleet, about thirty-five miles from Fraserburgh, and from a vessel fishing much further north, nearly sixty miles from port. On the second day the majority of the fleet aggregated on to the first of these two positions, but without any increase in the catches. Five boats, however, chose to steam to the more distant northerly position and they all took high catches (June 9th). There was no fishing on Saturday and Sunday June 10th and 11th but, when the boats returned to the northerly locality on June 12th, the catches had declined to a low level. The fleet continued to fish the northerly part of the area with only moderate success until June 15th when an isolated boat, fishing thirty miles to the south of the main concentration of boats, took a catch of over twenty crans. Immediately, the whole fleet aggregated on this position and, on June 16th, two-thirds of the catches were greater than twenty crans. The catches in this position subsequently declined and the boats once again dispersed. On June 20th there was a high catch on the north-western edge of the fleet, which led the fishermen in that direction, where catches greater than fifty crans were obtained on June 21st. As in the two previous cycles, the apparently profitable locality did not provide a third night of high catches, for on June 22nd, most of the catches were less than twenty crans, but boats on the edge of the fleet and well away from recently fished grounds were taking over fifty crans each.

It is easy to find many examples of this cycle of searching and exploiting, indeed it is difficult to find sequences which did not in some degree fall into this pattern; the example shown in Text-fig. 11 was selected at random.¹ In 1951, information about catches was collected by the Scottish Home Department and included all the landings at Fraserburgh and Peterhead; there were too many catches to show, in one illustration, the position of each individual boat and the size of each catch. The dots in Text-fig. 11, therefore, represent the number of boats fishing in each of the five-mile squares shown in Text-fig. 1 and the arrows indicate the top catch landed at each of the two ports. The same cycles are apparent, as in the previous illustrations; the aggregation of boats for a few days, followed by dispersal and subsequent aggregation on to a new position, which was usually discovered by a boat fishing in isolation or at the edge of the fleet. For example, pioneering skippers guided the fleet to new positions on June 5th, 7th, 12th and 13th, 1951. As in the previous example, there is evidence that, offered the prospects of good fishing near to and far from port, the fishermen, not unnaturally, select that nearest to their market. This is apparent in Text-fig. 11 when an isolated catch far to the north-east on June 12th attracted only three boats on the next night whereas a smaller catch, less than half as far from Fraserburgh, attracted a fair proportion of the fleet. The distant north-eastern position yielded very high catches for the second night in succession, but still it only attracted twelve boats

¹ The period centred on the birthday of one of the authors was selected for illustration.



TEXT-FIG. 11.—Charts showing the distribution of fishing vessels during nine successive nights' fishing in 1951. All the boats which landed at Fraserburgh and Peterhead are included. Each dot represents one boat, the dots being arranged symmetrically about the centres of the five-mile squares in which the boats fished. Arrows indicate the top catch landed at Fraserburgh and the top catch at Peterhead for each night.

when the nearer, and apparently less productive, locality had nearly forty boats fishing in close proximity to each other. On the penultimate day of the period illustrated in Text-fig. 11 the best catch, taken over sixty miles from port, was only forty crans and the next three catches were each less than twenty crans. Most of the fishermen consequently disregarded these indications and there was a wide dispersal of boats searching for new shoals of fish.

Four features of the searching habits of the fleet are relevant to a consideration of the use of fishing vessels as research ships.

1. Being guided by high catches, usually taken by solitary vessels, the fleet probably keeps in fairly close contact with the shoals of herring.
2. A single "patch" of productive fishing seldom lasts for more than three nights of exploitation by crowded vessels. As a result the fleet is constantly on the move from place to place.
3. As a result of the shifting foci of aggregation and because the fleet appears to disperse when contact with the fish is lost, a wide area of sea is sampled during the course of each week's fishing.
4. Distant grounds, which may well be populated by herring shoals, are not fished when there are alternative and perhaps less productive shoals closer inshore. This limitation of sampling only applies to drift-net vessels which, like those used in the present surveys, return to port each day to discharge their fish. English and Dutch drifters, which remain at sea for long periods do, in fact, explore much further afield than the Scottish boats.

AN ANALYSIS OF SUCCESS IN FISHING

The fishermen appear, therefore, to be influenced in their choice of grounds by relatively high catches which are often taken by a single vessel fishing in isolation, far from the fleet concentration. Were these high catches randomly distributed among the fishermen or did some skippers get more than a "fair" share? Were some fishermen in the habit of fishing in isolation from the rest of the fleet, and if so, were they more successful than their gregarious colleagues?

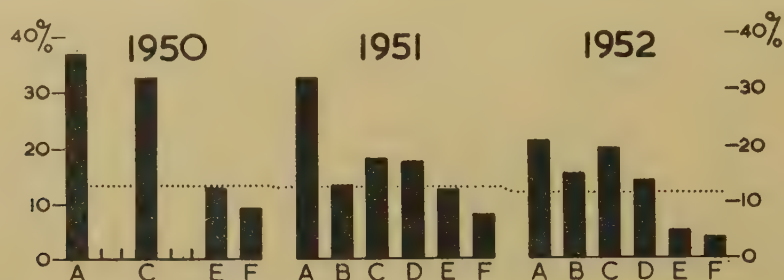
To provide answers to these questions, the performances of six skippers ("A"-"F") were analysed. Skipper "A", a most successful fisherman, was selected so that his record could be compared with five others who were chosen at random.¹ Skippers "B" and "D" seldom fished from Fraserburgh in 1950 and their performances in that year have not, therefore, been considered.

Text-fig. 12 shows the percentage of each vessel's catches which were twice, or more than twice, the average catch by all Fraserburgh vessels on the day of landing. The dotted line shows the percentage of *all* Fraserburgh catches which

¹ The names of all boats fishing at Fraserburgh in 1951 were arranged in alphabetical order. Letters of the alphabet were drawn at random from a hat, each paired with a number drawn from another hat. For example, if "H" and "6" were drawn, the selected fisherman was the Skipper of the sixth boat in the list of vessels whose name began with "H".

were twice the contemporary average. Skipper "A" frequently took the kind of catch which might be expected to influence his fellow fishermen; Skipper "C" was almost as successful, "E" was less so and "F" consistently took fewer than the expected number of high catches. The performances of these fishermen stood in the same relationship to each other in every year. Of the four who were fishing for all three years, Skipper "A" had most high catches, "C" was next, then "E", and "F" had least; in both 1951 and 1952 Skippers "B" and "D" had fewer high catches than "A" and "C", but more than "E" and "F". (The code letters given to each skipper were arranged in alphabetical order roughly corresponding to their success as fishermen.)

The number of vessels fishing in the five-mile square occupied by each skipper was recorded on every occasion when he shot his nets. The incidence of catches could then be grouped into those from squares with 1-4, 5-8, 9-12 ... boats

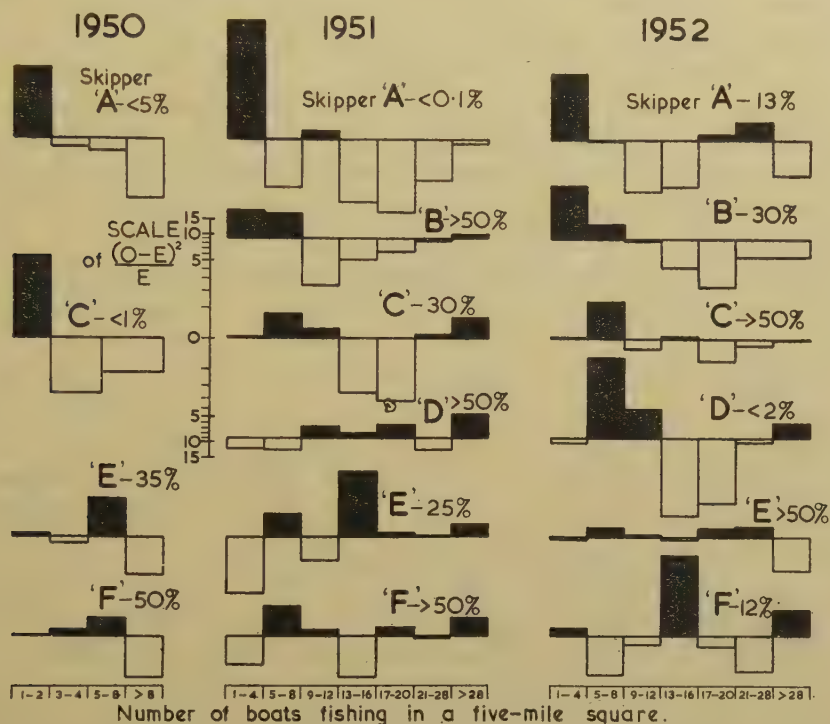


TEXT-FIG. 12.—Histograms showing the percentage of each of six skippers' catches which exceeded twice the contemporary average catch at Fraserburgh. The six skippers are identified by the letters A-F. The percentage of *all* Fraserburgh landings which exceeded twice the contemporary average catch is shown by the dotted line.

per square. In 1950, when information was collected from less than half the fishing fleet, the size of the categories was halved, *i.e.* 1 and 2, 3 and 4 ... boats per square. It was then possible to compare the observed frequency at which each skipper fished in squares occupied by different numbers of boats, with the expected frequency calculated from the distribution of the whole fishing fleet at Fraserburgh and Peterhead in 1951 and 1952, and at Fraserburgh only in 1950. The goodness of fit between the observed and expected frequencies was tested by computing χ^2 for each skipper individually, for the sample fleet of six boats and for the sample fleet of five randomly selected boats. The probabilities of the individual values of χ^2 and the class components of these values are illustrated in Text-fig. 13; each histogram represents the quantity $(O - E)^2/E$ where O is the observed and E the expected frequency of fishing in each class. The results are arranged with histograms above the line to indicate the classes in which observation exceeded expectation; histograms below the line represent the classes in which the observed frequency was less than the expected value.

It is clear from Text-fig. 13 that the skilled Skipper "A" fished by himself or with only two or three other vessels far more often than did the rest of the fleet.

Skippers "E" and "F", who got less than the average share of high catches (see Text-fig. 12), seldom fished by themselves, but preferred to find a crowd of their fellow-fishermen before shooting their nets. There is, in Text-fig. 13, an approximate series from "A" to "F" in which the peak histogram, indicating the most frequent incident, moves from left to right towards greater and greater aggregation. In 1952, for example, "A" and "B" preferred to fish in squares



TEXT-FIG. 13.—Histograms showing the frequency with which six skippers (A-F) fished in squares occupied by different numbers of vessels, compared with the expected frequency calculated from the whole fishing fleet.

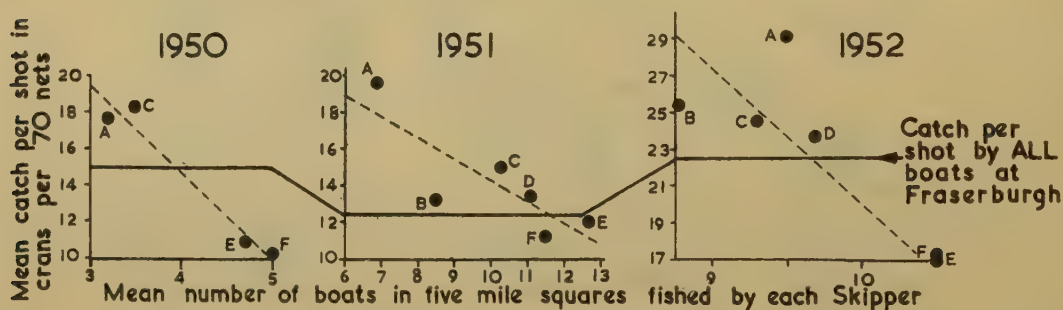
The goodness of fit was tested by χ^2 , see text, p. 162, for detailed explanation. The histograms show the individual class components of χ^2 , i.e., the value of $(O - E)^2/E$ in each class. Black histograms above the line indicate that the observed frequency exceeded the expected value; open histograms, below the line, indicate that observation was less than expectation. The probability of χ^2 (goodness of fit) is shown as a percentage against each skipper's code letter.

with less than 4 other boats, Skippers "C" and "D" preferred squares with 5-8 boats, Skipper "E" fished most often with 21-28 boats and "F" chose squares with 13-16 and with more than 28 boats.

For the combined group of five randomly selected skippers, the interaction χ^2 (6%, 60% and 13%) and the pooled χ^2 (12%, 50% and 40%) were non-significant in all three years, suggesting that these five men were, together, a satisfactory sample of the whole fleet in respect of the frequency with which they occupied

squares fished by different numbers of their colleagues.¹ The same test can be applied to the group of all six skippers, including the non-randomly selected "A"; in 1952 the results again suggest a non-significant departure from expectancy (interaction—13% and pooled —20%). In 1950, however, the pooled χ^2 ($P = 2\%$) suggests significant departure from the expected frequency and in 1951 the interaction χ^2 ($P < 2\%$) suggests considerable heterogeneity within the group of six men. The sources of these departures from expected fishing practice can be seen in the probabilities for the individual χ^2 in Text-fig. 13; it is clear that Skippers "A" and "C" in 1950 and "A" alone in 1951 did not fish the variously populated squares with the frequency to be expected from the results of the whole fishing fleet. It is also clear that these two skippers were atypical in so far as they preferred to fish in squares with small numbers of boats. It was seen above that these two men, "A" and "C", but particularly the former, were the men who consistently took more high catches than their colleagues.

Text-fig. 14 emphasizes the relationship between success in fishing and the tendency to fish in solitary isolation. The average catch taken by each skipper



TEXT-FIG. 14.—Dot diagrams showing the relationship between the mean catch per shot obtained by each of the six skippers (A–F) and the mean number of vessels per night in squares occupied by each of the six. The broken lines show the linear regression of "mean catch" upon "mean number of vessels per square".

during each season is plotted against the average number of vessels in each five-mile square fished by each skipper. There was a significant inverse linear relationship between the two variables; fishing success declined with increasing gregariousness (the correlation coefficient, r , showed significance at $< 1\%$, $< 5\%$ and $< 2\%$ in the three years respectively). The calculated linear regression of "catch" upon "number of vessels per square" is shown in Text-fig. 14.

The evidence provided by these six fishermen, therefore, suggests that very high catches were not randomly spread amongst the boats. Those who took more than their "share" of such catches preferred a solitary role, and these were the men who, by their success, were likely to influence their fellows in the choice of fishing grounds. The evidence suggests also that each fisherman had his own character-

¹ For an account of the use of pooled and interaction χ^2 , see Snedecor (1946, pp. 191–192).

istic technique, which he consistently maintained in different years; some were consistently gregarious and relatively unsuccessful, others were consistently solitary and these were the successful men. It should be emphasized that the gregariousness of a skipper is here compared with his overall fishing success; it is not implicit that all solitary fishing yields high catches, indeed it will be demonstrated below that this is not so.

CATCH FLUCTUATIONS AND THE AGGREGATION OF VESSELS.

Fishermen sometimes express the opinion that the best shots are often taken at the edge of a concentration of vessels. Boats fishing in the centre of such a concentration are believed to miss fish which are "screened" by the nets of other boats fishing close to them. It is also apparent, from an inspection of the catch statistics, that the average catch in a specific locality tends to decline more often, compared with the previous night's fishing, when the locality becomes crowded with vessels. An example may be seen in Text-fig. 10 where, on June 9th, five boats fishing in the extreme north of the area took high catches, but when the rest of the fleet subsequently crowded into this area, on June 12th, the average catch fell to a very low level. The same Text-figure provides another example. A profitable locality was found by a single boat on June 15th; for three nights the fishing fleet aggregated on this position with high catches on the first night, smaller on the second and with only moderate results on the third night (June 20th).

To test this impression of declining catch with increasing aggregation of vessels, two areas, each 10 miles square, were subjected to detailed analysis. The two squares were selected from that part of the area which was most consistently fished throughout the season. The 10-mile squares were both taken from the International square C 15; they were each composed of four neighbouring five-mile squares and may be identified from Text-fig. 1:

Square *i*: C 15—five-mile squares 27, 28, 33 and 34 (over Bosie's Bank).

Square *ii*: C 15—five-mile squares 29, 30, 35 and 36 (immediately to the east of Bosie's Bank).

The method of collecting statistics prior to 1951 was limited to Fraserburgh and was extremely inconsistent. In 1947 the landings of a very small number of vessels were recorded; the collection of market statistics was begun at the end of June, 1948, and subsequently a variable proportion, never more than half of the Fraserburgh landings, was recorded from those catches which were sold in the market. On the other hand, complete statistics are available from the Scottish Home Department's collectors at Fraserburgh and Peterhead during the period 1951–54. For these reasons, and because only square *i* was consistently fished in the period 1947–50, the material for 1951–54 only was used in the statistical test which follows.

The average catch per vessel was calculated for each of these two squares for every night on which boats fished there. Whenever a square was fished for two or more successive nights, the average catch in the square on the second and each subsequent night could be expressed as a decrease or an increase of catch compared with the results of the preceding night's fishing. Each decrease or increase of catch could then be associated with (a) the number of vessels fishing in the square on the previous night and (b) the number of vessels in the square on the same night. To take an example from square *ii*; on July 15th, 1952, there were 27 boats in this square with an average catch of 35.5 crans per shot. On the next night, July 16th, there were 5 boats with an average catch of 16.0 crans. This result is classified as a decrease in catch associated with (a) 27 boats on the night preceding the decrease and with (b) 5 boats fishing in the square on the same night as the decrease.¹

The incidence of decreases and increases was then grouped according to the number of vessels, *i.e.* 1-4, 5-8 ... vessels in the 10-mile square. The hypothesis of no association between catch fluctuations and the number of vessels fishing in the square was then tested, by χ^2 in a " $2 \times n$ " table in which the "2" entries were "Increases" and "Decreases" of average catch and the " n " entries were the classes 1-4, 5-8 ... vessels in the square. The analysis was performed with the results classified according to the number of vessels fishing in the square (a) on the preceding day and (b) on the same day as the decrease or increase of average catch.

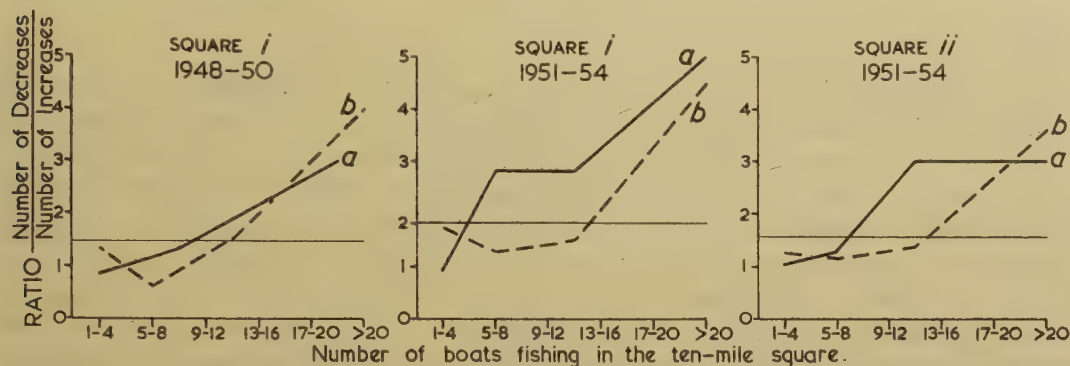
The values of χ^2 for both areas *i* and *ii* were non-significant when catch fluctuations were classified (b) according to the number of vessels fishing in the square on the same day ($P > 25\%$ and $> 10\%$ for squares *i* and *ii*, respectively). The values of χ^2 ($P < 1\%$ and $< 4\%$) for the alternative classification (a) suggest that there was a significant association between catch fluctuations and the number of vessels fishing in a square on the day *preceding* the increase or decrease of catch per unit effort.

The form of the association between catch fluctuations and the aggregation of boats is seen in Text-fig. 15. This shows the ratio, "number of decreases divided by number of increases of catch", plotted against the number of vessels fishing in the square. Some of the groups "vessels in the square" have been combined; these are the combinations which were used to ensure that the expected frequencies in the cells of the " $2 \times n$ " table were not less than five. The thin horizontal lines in the graphs give the overall ratio of decreases to increases, independently of the number of vessels fishing in the square, *i.e.* the ratio which would be expected if there were no association between catch fluctuations and the aggregation of boats. The results from square *i* during the period 1948-50 are shown on the same basis because, although the data for this period were too incomplete for precise analysis,

¹ Out of a possible 356 catch fluctuations in these squares, only seven showed "no change", *i.e.* the average catch was the same on two successive nights; on four of these seven occasions the average catch was nil crans per vessel. These seven results have been ignored in the analysis.

they illustrate that a similar trend was evident throughout the whole period of the survey.

It is clear, from Text-fig. 15, that there were more increases than expected at the lower levels of fishing effort and more decreases than expected when the vessels crowded into the area. This effect is most marked, as the χ^2 values suggested, when catch fluctuations are compared with the previous day's effort, but the effect is also evident in all three graphs for the comparison between catch and the effort on the same day.



TEXT-FIG. 15.—Graphs showing the ratio “number of decreases of catch divided by number of increases” plotted against *a* the number of vessels fishing in the square on the night preceding, and *b* (broken line) the number of vessels fishing in the square on the same night as the increase or decrease of catch. See text, p. 166, for further detail. The thin horizontal line shows the overall ratio of decreases to increases, irrespective of the number of vessels fishing in the square.

To summarize, it appears that increasing aggregation of fishing boats is accompanied by a decrease of catch per unit effort; crowding of fishing boats appears to affect the contemporary catch, but the effect on the following day's fishing is more marked and is detectable at a lower level of aggregation.

A falling catch with aggregation of vessels may suggest a high fishing mortality, but many fishermen believe that mechanical interference with the herring shoals may result from the presence of a concentration of boats with their miles of drift-netting. It must also be remembered that the fish are not uniformly dispersed over a wide area of sea; echo-sounder surveys off the Scottish coast suggest the presence of small discrete shoals. It may be that there is a limit to the number of boats which can shoot their nets directly over a shoal or over a patch of several shoals. Even if fishing mortality was insignificant one might find that, say, four or five skippers would be free to manoeuvre their boats over the fish and, if these boats remained alone, the mean catch would be high; if another five boats arrived they might not be able to get nearer than the edge of the shoal and the average catch for the area would be depressed. The next five boats might be quite outside the shoal of fish, even though they crowded as closely as possible to the boats already lying with their gear shot, and the apparent effect of crowding would be a reduction

of the catch per unit effort. This type of catch limitation would affect the catches on the same day as the crowding of vessels, *i.e.* the analysis (*b*) above. Although the association between aggregation of boats and decrease of catch was non-significant on the "same day", it is apparent, from all three graphs (*b*) in Text-fig. 15, that there were over twice the expected number of decreases in catch when more than 20 boats fished in a 10-mile square.

DISCUSSION.

Limitations of the area sampled.

The collection of landing statistics has made clear the limitation of area which is imposed when samples are collected from fishing vessels. There is a suggestion that the Scottish boats may not have fished in the centre of the distribution of the herring stocks; the boats might have taken higher catches if they had steamed further offshore where Dutch vessels were usually fishing (pp. 145-147). Cushing (1952), also, noticed that drifters (from North Shields) fished on the inshore edge of the concentration of herrings which was detected by echo-sounder from a research ship. This type of restriction of the fished area is not simply the result of the limiting range of the size and type of fishing boat. The fisherman's object is to obtain the maximum financial profit from his efforts; depending on the market demands and prices, this may not always mean the collection, from the sea, of the greatest possible number of crans of herrings. Generally, if there is a demand for fresh fish, boats will tend to select grounds near the home port even if there are indications of high catches further offshore. Fluctuations in the price of fish meal, coupled with the changing demand for fresh herrings, may have caused the fishermen, in 1952, to exploit the more distant grounds which they had neglected in previous years (pp. 145, 146).

Samples collected by fishing boats are therefore drawn from an area the limits of which may change from year to year for reasons which may have nothing to do with biological fluctuations. Samples may be lacking from an area which is known to contain herrings.

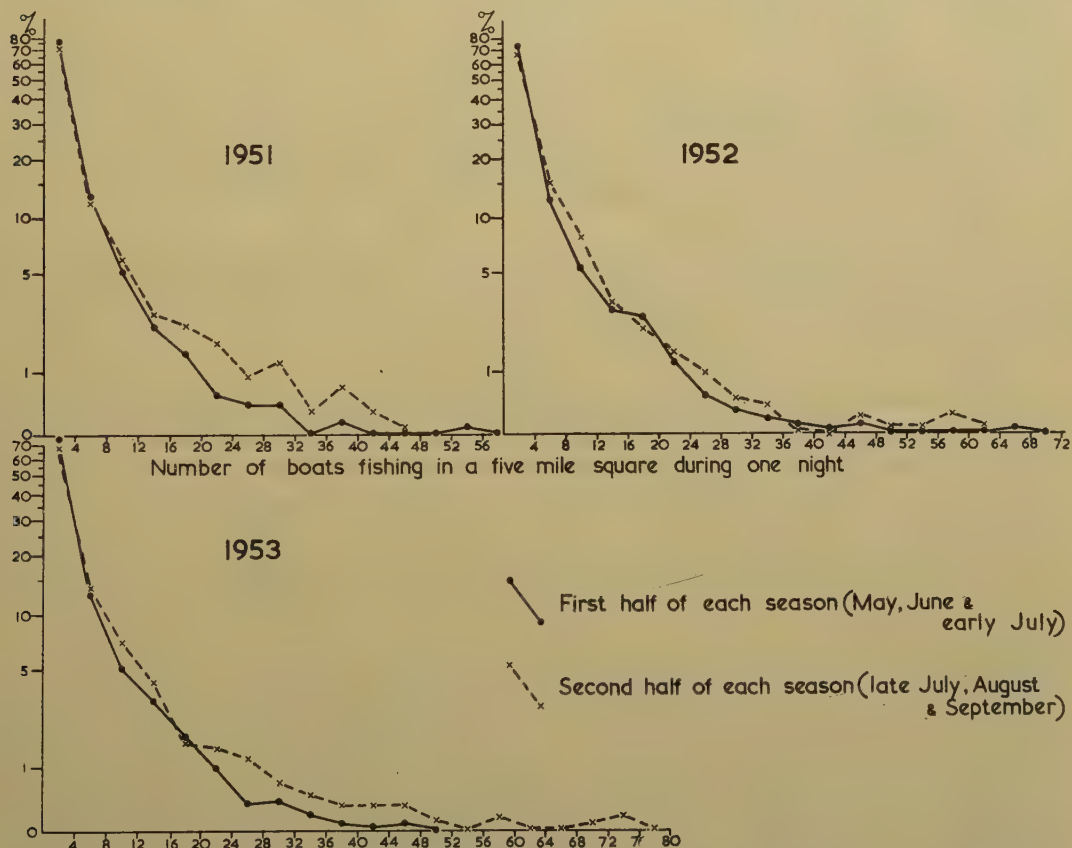
Another factor which affects the area sampled is the fishermen's traditional preference for certain localities at certain characteristic times of each year; a three-phase season has been postulated on the basis of the locality which was fished. As a result of this, more samples may be expected from the northerly part of the area in May than in August and the more distant easterly area will probably be better sampled in July than in May and August. Although there was a traditional pattern of fleet aggregation during each season, in fact the vessels explored a wide area of sea in the course of their search for shoals of herrings. The composition and distribution of the fleet changed from day to day, some boats taking up the role of searchers looking for new shoals while the rest aggregated on to a previously discovered patch of herrings (pp. 158-161). Therefore, although many of the samples taken by fishing boats during any one night may come from a restricted

area, one may, in fact, expect a fairly wide spread of sampling in the course of, say, a week's fishing.

The significance of the area limitation imposed by sampling from fishing boats may be assessed when these samples are compared with those taken from research ships of the Scottish Home Department which, at monthly intervals, surveyed the area with a considerable extension beyond the boundaries of commercial fishing.

Aggregation of fishing boats.

During the years 1951 to 1953, when all the catches from the Fraserburgh and Peterhead fleets were plotted, there were between 10,000 and 15,000 landings in each year; of these 9.2% in 1951, 9.0% in 1952 and 9.1% in 1953 came from boats which were fishing alone (during one night) in a five-mile square. Or, the squares which were occupied, during one night, by only one vessel formed 42.5%, 40.0% and 41.5% of the 2,400 to 3,200 incidents in each year when a five-mile square was fished. Text-fig. 16 shows the percentage frequency distributions of



TEXT-FIG. 16.—The percentage frequency distribution of five-mile squares fished by different numbers of boats during one night's fishing. The material relates to all landings at Fraserburgh and Peterhead,

the squares fished, during one night, by different numbers of boats. The same grouping is used as previously, *i.e.* 1-4, 5-8, 9-12 . . . boats in a five-mile square. The material has been divided into two halves, before and after mid-July; this effectively divides the season into an early half, when the herrings were feeding actively, and a second half, when the fish were sexually mature or spawning. There is close similarity between the frequency curves for the three years, a high proportion, about 70%, of the squares in each year being occupied by less than 5 boats in a night's fishing. The incidence of crowded fishing was greater during the second, or spawning, phase of each year than during the earlier, feeding phase. For instance, in 1951 about 12% of the landings in the first half but over 27% of those in the second half of the season came from squares with more than 20 vessels; the comparable figures in 1952 were 17% and 25%, whilst in 1953 about 15% in the early part and 32% of the landings in the later part of the season came from squares crowded with more than 20 boats.

Cushing (1952) discussed the difference between spawning and feeding shoals in relation to echo-surveys of fish; he thought that the shoaling distribution might be different during these two phases because spawning fish occur in large shoals, whereas feeding fish occur in small ones. It may be that the wider dispersal of boats during most of the summer season indicates the presence of a number of scattered shoals of herrings which are presumably feeding. The restriction of the fished area and the greater concentration of fishing boats in the later part of the season may, therefore, reflect the aggregation of the small shoals of feeding herrings into a few large spawning shoals.

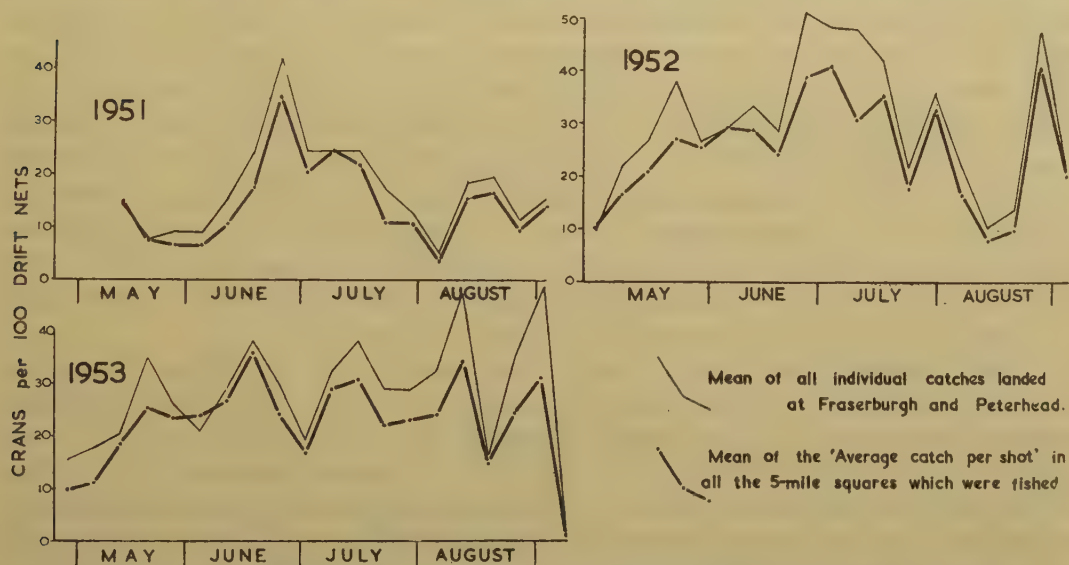
The varying aggregation of fishing vessels can affect the estimate of the natural population of herrings which is derived from the size of the catches. This estimate is also complicated by the possibility that the catch may decline as the result of heavy fishing by a concentration of boats (pp. 166-168).

The evidence for a decline in catch following aggregation of boats was derived from an analysis of the succession of events in one specific locality and as such it provides a comment on the biology of the herring. Fishermen, however, did not consistently exploit one specific locality; the centres of aggregation of the fleet shifted rapidly from place to place (pp. 158-161). The fishermen are certainly aware of the short-lived duration of successful fishing in one locality. It is probable that, as a precaution, the fishermen disengage from a patch of herrings *before* the catch falls appreciably. They are unlikely to concentrate in one place after the catch there has fallen below the average for the whole area. The usual signal to disengage from a patch seemed to be the discovery, elsewhere, of a likely shoal of fish, a discovery which was often made by a single boat isolated from her fellows.

If, therefore, the fish are not evenly distributed over the whole area, the shifting positions (coupled with the varying degrees of concentration of the boats) may invalidate the simple "average catch per unit effort" as an expression of the overall density and of fluctuations in the density of the herring population. It is usual to correct this bias by calculating the catch per unit effort in sub-areas; a

new density index can then be obtained by averaging the catches per unit effort from each of the sub-areas, instead of averaging all the individual catches. This practice has sometimes been used in the present work, where the sub-areas are the five-mile squares shown in Text-fig. 1.

Gulland (1955) shows the density indices for North Sea haddock as determined by the simple catch per unit effort and by the corrected figure derived from the sub-area mean catches. The mean of all individual catches was about 15% higher than the mean of the sub-area mean catches, indicating a "small and relatively constant degree of concentration of the fleet on the haddock". Text-fig. 17 shows, week by week, the two estimates of herring catch during the three years when complete landing statistics were available from Fraserburgh and Peterhead. The simple mean of all the catches was, on average, about 24% higher than the mean of the square means. This implies that, as one would expect from an efficient fleet, the boats concentrated on to the fish. The degree of concentration, as can be seen from Text-fig. 17, was fairly constant, although there was a period of four weeks



TEXT-FIG. 17.—Two estimates of the abundance of herrings determined from the commercial landings at Fraserburgh and Peterhead in 1951, 1952 and 1953.

in 1952 when the difference between the two estimates was of the order of 40% and, during the first fortnight of 1953 and for two weeks at the end of August in the same year, it was more than 50%.

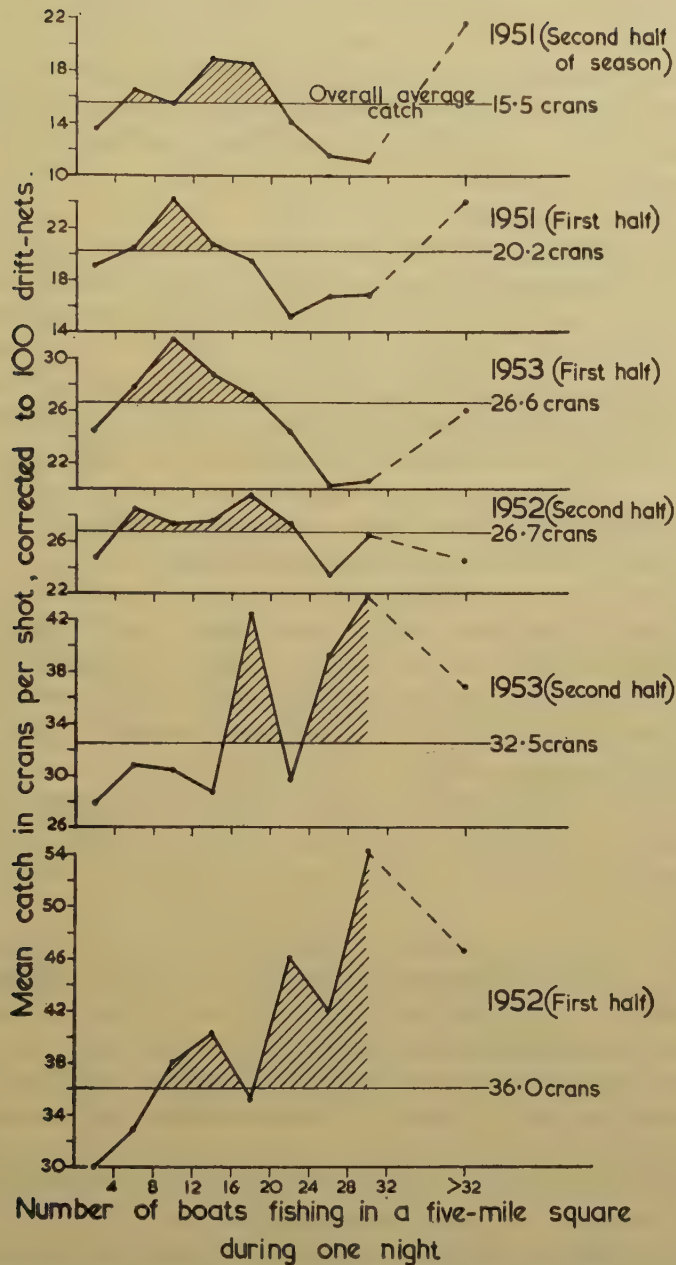
Cushing (1953) has studied the relation between the mean catch per shot in ten-mile squares and the number of vessels fishing in the squares.¹ He found that the catch decreased with increasing aggregation of boats in May at North

¹ See also Cushing (1955) which was published after the present paper was written.

Shields, where the overall average catch at the port was about 6 crans per shot. Off East Anglia in October, where the overall average was about 36 crans, there was no relation between number of boats and average catch, but in November off East Anglia, where the overall average was 52 crans, the greater the number of boats in a square the greater the mean catch. These three results of aggregation seemed to be related to the abundance of fish as evidenced by the average catch at the port. The technique used by Cushing has been employed in Text-fig. 18. Results from Fraserburgh and Peterhead during each of the seasons 1951, 1952 and 1953 have been divided again into the early, feeding period and the late, spawning period, *i.e.* before and after mid-July. All the catches in each five-mile square were recorded for each night's fishing; the results for each half-season were then combined in categories according to the number of boats fishing in the squares, using the groups 1-4, 5-8, 9-12 . . . etc., boats in a five-mile square during one night. The mean catch per shot was then calculated in each of these categories. Following Cushing's suggestion of an association between aggregation and the overall abundance of fish, the graphs in Text-fig. 18 have been arranged in sequence, according to the overall average catch, with the lowest (15.5 crans in the second half of 1951) at the top and the highest (36.0 crans in the first half of 1952) at the bottom of the text-figure. The last point on each graph, the mean catch in squares with more than 32 boats, usually represented only one or two occasions when a square was occupied by a very high number of vessels; for this reason the line of the graph to these points is broken. Such heavy concentrations of vessels probably occur on the rare occasion when a very dense shoal of herrings is so obvious that no one can miss it. The first two points on each graph, which show a low catch per shot, probably represent the searching part of the cycle—squares with few boats, many of them unsuccessful in detecting herrings.

The remaining points on the graphs, for squares with more than 8 and less than 32 boats, may be considered to reflect the effects of aggregation of fishing vessels. The tendency in the top three graphs, when the overall mean catch was relatively low, was for a decline in catch with increasing aggregation of boats. In the graph for the second half of 1952 the catch appears to be independent of aggregation, but the last two graphs, when the overall mean catch was high, suggest an increase of the catch per shot with increasing concentration of vessels in a five-mile square. The peak catch per shot was at 13-16 boats per square in the second half of 1951; the corresponding peaks, reading downwards in the illustration (*i.e.* with progressively increasing overall catch) were at 9-12, 9-12, 17-20, 29-32 and, in 1952 (first half), at 29-32 boats in the five-mile square.

It should be emphasized that graphs of the type shown in Text-fig. 18 and used by Cushing (1953) do not indicate the effect on the catch of aggregation of boats which was demonstrated earlier (pp. 165-168). Instead the graphs reflect the interaction of movement and aggregation of the fish with movement and aggregation of the fishing fleet; in other words, the efficiency of the searching and catching techniques. Text-fig. 18 provides support for Cushing's suggestion that fishing



TEXT-FIG. 18.—The mean catch per shot in squares occupied by different numbers of boats, using the combined Fraserburgh and Peterhead landing statistics. Each season has been divided into an early and a late half; the half-seasons are arranged in sequence according to the size of the mean catch per shot, by all vessels; the half-season with the lowest mean (15.5 crans) is at the top, and that with the highest (36.0 crans) at the bottom. The hatched part of the graphs indicates values greater than the overall average catch per shot for each half-season.

efficiency is dependent on the relation between the number of available fish and the number of fishing boats. One cannot, however, determine whether a decrease of the mean catch, with increasing number of boats, results from fishing mortality, from mutual screening of the shoals by drift-nets, from natural migration of the fish, or from a migration or dispersal of the fish resulting from interference with the shoals by a concentration of boats.

The evidence, so far, suggests that :

1. Successful skippers tend to fish more often by themselves than their less successful fellows ; the mean catch per vessel declines in an area which is fished for two or three consecutive days by moderate or large numbers of boats.

2. Within the area which is explored, the fleet concentrates successfully on to the fish, in other words, squares with few vessels produce a lower average catch than squares with moderate or, sometimes, large numbers of boats.

At first sight, these two conclusions appear to contradict each other ; the following thesis shows that there is, in fact, no conflict.

Isolated boats, in general, catch fewer fish than concentrated boats. Some lone fishermen, however, are more skilled than others and often take the high catch which shows the fleet where to aggregate on to the fish. Concentration of vessels for long in one place tends to reduce the mean catch *in that position*, but the fleet is able to avoid the worst effects of such localized decreases. This is achieved by constantly shifting the regions of fleet concentration.

When the fish are scarce, relative to the number of vessels, the searching and aggregating processes are less successful than when the fish are abundant ; the optimum number of vessels, per statistical square, declines with decreasing abundance of herrings.

Squares with less than five boats constituted about 70% of the total number of squares fished. There are two reasons for lone fishing, (i) the desire to search for new shoals of herrings and (ii) failure to find the known shoals. Lone fishing probably approximates to a random distribution of vessels with regard to the shoals of fish, but there may not be a random distribution of high catches among the isolated boats searching for new shoals. Some skippers are probably more skilful at reading the "appearance" of the water and in using the echo-sounder. These skilful men will tend to get high catches even when they fish on their own, whereas most of the skippers will only be confident of taking what, for them, would be high catches when they act on previous information and concentrate on a recently discovered patch of fish. Some, perhaps most, isolated fishing may be the result of less than average skill because a man misreads the "signs" and takes up a fishing position where no other skipper can see any indication of herrings. Since the nets must be shot before nightfall there is a limit to the amount of searching which can be done ; it is common to hear a skipper say that, having found no sign of herrings,

he was compelled by the lateness of the hour to shoot his nets and trust to his luck.

Graham (1931) discussed the possibility that the shoals of herrings were subject to interference by drift-nets. He came to the conclusion that "normally" the herrings could see the nets and could swim round, above, below and alongside them, so that "the sea may be full of herring, yet none caught". At times, however, Graham thought the herrings were influenced by crowd excitement caused by panic or by sexual or migratory impulses; at such times the fish were oblivious to the nets in which they were caught, often in immense quantities. He concluded that neighbouring boats did not screen each other's nets because the fish were probably interspersed between the fleets of drift-nets; at the times of excitement or panic herrings blundered, so to speak, into the nearest net to the southward, since their tendency at such times was to migrate to the south. Graham's observations were restricted to East Anglia; in Scottish waters the sea is much deeper and the boats do not crowd so closely together as in the East Anglian fishery. Most of the fish caught off Lowestoft and Yarmouth have stopped feeding prior to spawning, whereas, for at least half of the Scottish season, the herrings are actively feeding. It may be connected with the difference between the two fisheries that the echo-soundings suggest the presence of small, discrete and tightly packed shoals in Scottish waters, whereas the East Anglian fish are probably more evenly dispersed.

It is difficult, therefore, to apply Graham's hypothesis of herring behaviour to the Scottish summer fishery. Scottish fishermen believe, and casual observation suggests, that the nets of one boat may sometimes take a shoal of fish and prevent it from reaching the neighbouring boat's nets. Fishermen's accounts of the distribution of fish along the fleets of nets from neighbouring boats often appear to fit a "screening" hypothesis. Such evidence is difficult to assess, however; the kind of fishery statistic which is available does not permit a sufficiently detailed study of the catches of individual boats. Information is badly needed on the relative positions of the nets of neighbouring boats, the direction of the tide and wind, the amount of drift through the water and the size of the catch with details of the distribution of the fish in the nets. Graham (1931) provides four plots from information of this type, but the compilation of such details must be a slow task. A reserve of trained fishermen who might be paid for such information would speed the work.

In considering the behaviour of the herring there are few refined experimental results to give the clues. One is compelled to collect information from the fishing fleet and at intervals take stock of the accumulating theories. Great progress might be made if it were possible to direct the fishing fleet or a part of it. Boats might be sent to unexploited areas, or might be directed to a locality in which traces had been seen on the echo-sounder of a research ship; some skippers might be directed quite randomly providing a control to test the part played by skill in fishing as well as building up a picture of the overall abundance and distribution of the herring and its environment.

SUMMARY.

1. Professor A. C. Hardy's work on the herring and its animate environment has been continued and extended in a long-term study of the Scottish summer drift-net fishery. The work is part of a joint programme shared between the Scottish Home Department's laboratory at Aberdeen and the Scottish Marine Biological Association's laboratory at Edinburgh.

2. Most of the information about the environment and all the samples of herrings were collected from commercial fishing vessels in the course of their normal activities. As a preliminary to the work on herring ecology, therefore, it has been necessary to study the characteristics and limitations of this method of collection.

3. The fleet usually fished on the inshore edge of the natural population of herrings; higher catches would probably have been taken if the boats had fished further offshore (pp. 145-147). For economic reasons, the distant grounds were seldom fished when there were alternatives nearer home (pp. 158-161). Fluctuations in market demands and prices may result in changes of the area sampled by the fishing fleet (p. 145).

4. Boats from Fraserburgh and Peterhead found their best fishing progressively further south in each successive year from 1947 to 1954. This southerly shift, coupled with the increasing success of these ports relative to the fishing at Lerwick, suggests a progressive redistribution of the stock of fish during the period of the survey (pp. 146-150).

5. The fishing fleet explored the area in a fairly regular manner each year, first fishing over and near shallow banks, later over deep water and, towards the end of each season, progressively further southwards and shorewards towards the spawning grounds of the herring. It is suggested that the three phases may reflect three stages in the distribution and migration of different components of the herring stocks (pp. 150-157).

6. The techniques of searching for and subsequently exploiting the shoals of herrings are examined. The boats usually concentrated on the position of a previous high catch; such concentrated fishing seldom lasted more than two or three days in one place. The high catches which guided the fishing fleet to new shoals were often obtained by a single boat fishing in isolation away from all other fishing vessels (pp. 157-161).

7. An analysis of the records of six skippers shows that successful men fished alone more often than the less successful who generally shot their nets among a concentration of boats (pp. 161-165).

8. There is evidence that the average catch per unit effort declines in an area which is subject to heavy fishing effort. It is emphasized that this does not necessarily imply a heavy rate of fishing mortality (pp. 165-168).

9. Aggregation of fishing vessels was more marked in the later part of each season, when the fish were preparing to spawn, or were spawning, than in the

earlier part of the season, when herrings were actively feeding. This may reflect a difference in shoaling behaviour during the two phases of the herring's life cycle (pp. 169, 170). It is shown that the fishing fleet aggregated on to the fish (p. 171).

10. Although successful skippers tended to prefer solitary fishing, all solitary fishing was not successful; the average catch in statistical squares with moderate numbers of boats was higher than that in squares with few boats. It is presumed that of the many scattered searching skippers most were unsuccessful but that a few men were consistently skilful at detecting shoals of herrings. Many, perhaps the majority of fishermen, got their best results from keeping with the fleet, exploiting previously discovered shoals (pp. 172-174).

11. By constantly shifting the focus of aggregation, the fleet avoids the effect of localized decreases in catch following heavy fishing. Efficiency of searching and fishing are dependent on the relation between numbers of fish and numbers of boats (pp. 172-174).

12. The characteristics of commercial sampling are discussed in relation to the limitation of area which they impose and with regard to the use of commercial catches as an index of abundance of fish.

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CONTINUOUS PLANKTON RECORDS:

THE DISTRIBUTION OF YOUNG *GADUS* *POUTASSOU* (RISSO)

BY

G. T. D. HENDERSON, D.S.C., PH.D., B.Sc.

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INTRODUCTION.

THE Continuous Plankton Recorder Survey was first extended beyond the limits of the North Sea in April 1939, when the "V" route between the Pentland Firth and Iceland was initiated. Although only six records were obtained before the war, young fish had been collected from over the deeper waters outside the 100 fathom line, and Lucas, Marshall and Rees (1942) state that the maximum numbers were caught in May, and that these were mostly gadoids (see their p. 84 and text-fig. 5). Later, the majority of these gadoids were identified as *Gadus poutassou* (Risso) and the species was included by Stubbings (1951, p. 278) in the list of young fish identified during the pre-war survey.

In the early months of 1947 a few records were obtained in approximately the same area, but it was only when the weathership routes in the Atlantic were added, from 1948 onwards (see Rae, 1952, p. 136 and text-fig. 1), that wide and regular sampling to the west and north-west of the British Isles became practicable. It was evident by the end of 1949 that the young of *Gadus poutassou* were being caught

regularly in April and May (Henderson, 1954, p. 233 and text-fig. 4), at times in quite large numbers. Since 1949 catches have been obtained every year, and the material now seems adequate to support a study of some aspects of the distribution and abundance of the young stages of this species, with some indication of the possible fluctuations from year to year.

It seemed to be worth while re-examining the distribution of these young Poutassou, as the material on which Schmidt (1909) based his results was collected about fifty years ago, during the latter half of which period there has been a marked "warming up" of the waters of the North Atlantic (Smed, 1947 to 1954; Scherhag, 1937). Further, one cannot disregard the possibility that this widely distributed species, which is by no means the smallest of the gadoids, may yet become exploited commercially, in which case a contemporary account of the breeding and abundance of the young stages would be of considerable value. (Compare Tåning, 1949 on *Sebastes*.)

NOTES ON THE ADULT.

Gadus poutassou (Risso) appears to have had only two common English names, Couch's Whiting (for which see Couch, 1877) or Poutassou, which is the only name used by Schmidt (1909) and Travis Jenkins (1936). Ehrenbaum (1936) gives both names. Hickling (1927) however, refers to the species as "Blue Whiting" without quoting any other name, and "Blauer Wittling" is included as a German name by Ehrenbaum (1936) along with "Blågunnar" as a Norwegian name. In a private communication Dr. C. F. Hickling states that "Blue Whiting" is the name he has heard used by Fleetwood and Milford Haven fishermen for this species, which they encounter frequently when fishing for hake, and he suggests its more general use. The name is related to a predominant bluish tinge to the fish, especially when the scales are rubbed off.

Adult Blue Whiting may attain a length of 30 to 40 cm. (Jenkins, 1936, p. 153, Ehrenbaum, 1936, p. 117) and are taken by commercial fishing vessels, sometimes in large quantity in the Bay of Biscay (Schmidt, 1909, p. 88) and to a lesser extent in Norway (Ehrenbaum, 1936, p. 118). There is also a regular fishery in the Ligurian Sea, by steam and motor craft (Gualini, 1938). The quantities taken by British vessels, however, do not appear to have been large enough to justify a specific entry in the landing statistics, and are presumed to be included in the category "other kinds".

The distribution of the adults is stated by Schmidt (1909) to extend from the Mediterranean to the North Cape of Norway, and they are also found off the south and west coasts of Iceland (Saemundsson; 1949). Their distribution over the "Polar Deep" between Norway and Greenland, and Spitzbergen and Faeroe-Iceland is demonstrated by the large concentrations of otoliths found in bottom deposits which are discussed by Jensen (1905), while Boldovsky (1939) quotes occurrences of adolescents in the Barents Sea, for the period 1934 to 1938.

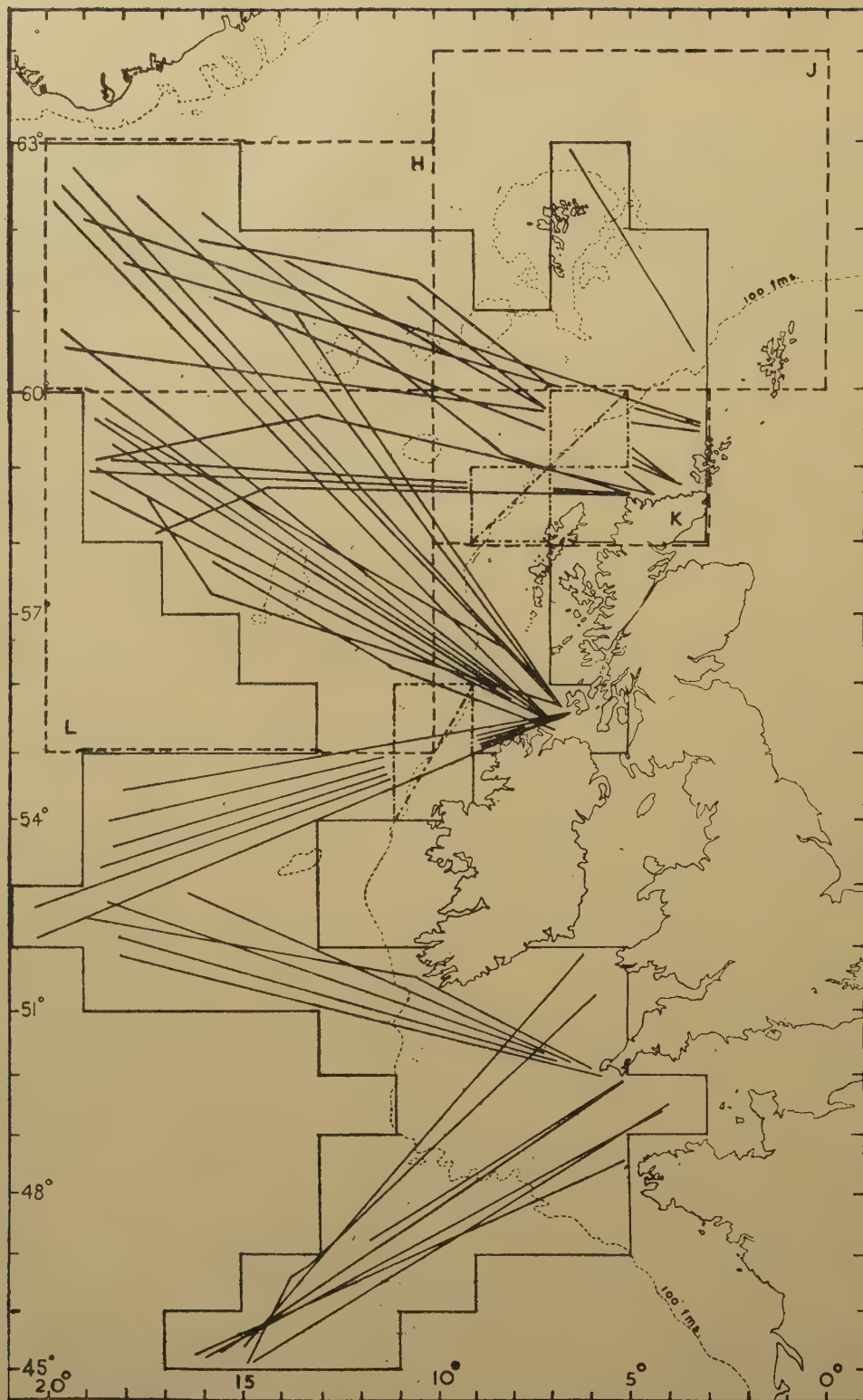
The adults do not appear to occur in appreciable numbers in the North Sea south

of latitude 59° N. (see Schmidt, 1909, p. 87, para. 4, and p. 151, Text-fig. 13); this is emphasized by isolated specimens caught in the North Sea being noted as unusual occurrences. The author has seen a specimen which was caught in a drifft net off Fraserburgh. Their great abundance within the normal limits of distribution is emphasized by Hickling (1927), who states (p. 42) that they form 36.6% by weight of all food eaten by the hake, and may amount (p. 47) to as much as 70% by weight of the food of hake caught in waters of 250 fathoms depth.

NOTES ON THE YOUNG.

The young stages are described and illustrated by Schmidt (1905, p. 57 *et. seq.*, plate III; 1906, pp. 11, 12, and plate), and these appear to be the first accounts of the larvae and post larvae of this species. The smallest individual he described was 6 mm. in length, so that a gap can be filled from the recorder material, which includes many as small as 3.5 to 4.0 mm. and a few of 2.7 to 3.0 mm. taken in 1955; these, and an egg capsule also found in 1955, will be described in detail on p. 198.

Schmidt (1905, 1906, 1909) has outlined the distribution of the young stages, and states that the recently hatched young (and by inference the spawning areas) are located in the Bay of Biscay, off south-west Ireland, to the west and north-west of the British Isles, and extending north-west from off the Hebrides to the waters south-west of Iceland; the north-eastern limit of this last area is clearly some distance south-west of the shallowest part of the Iceland-Faeroe-Scotland ridge. He states further that no young have been found in the Norwegian Sea and Skagerrak. None of the references consulted have extended the limits of distribution of the youngest stages suggested by Schmidt, although two add some detail for the adolescents. Boldovsky (1939) gives an account of the occurrence of adolescent *Gadus poutassou* in the Barents Sea from 1934 to 1938. Small numbers were found from 1934 to 1937, ranging in size from 5 to 15 cm. but in 1938 specimens of this size range were caught from the Nordkin and Nordcape Banks, from Finmark, from the south-west slopes of the Murman Bank, and as far as 40° E. longitude. For example, on April 10th, 1938, in the area of latitude 72° N. and longitude 26° to 27° E., a catch of 100 kgs. of 5 to 15 cm. individuals was secured; other similar catches are recorded in this year. Boldovsky suggests that these adolescents must have been brought into the area by the North Cape currents, as they do not spawn in the Barents Sea. Thus Schmidt's northern limit of distribution is somewhat enlarged for the adolescents. Saemundsson (1929) reports catches in N.W. Faxe Bay of *Gadus poutassou* of 18 cm. and upwards, but refers to the distribution of the younger stages " . . . off the warmer (S. and S.W.) coasts [of Iceland] ". This extends the distribution somewhat round to the west of Iceland as compared with Schmidt (1909). Saemundsson suggests a growth rate, indicating a length of 16 cm. at an age of one year, the implication of which is that the Barents Sea catches in April cannot yet be 1 year old, as the largest reported is only 15 cm., and the smallest are but 5 cm.



TEXT-FIG. 1.—Chart showing: (i) the boundaries of the area within which samples have been collected (—); (ii) the outlines of the four areas, H, J, K, L for which temperature anomalies are given by Smed (---); (iii) the outlines of the four subdivided squares, showing the relation of the dividing line to the 100 fathom line (·-·-·-); (iv) some representative tracks over which the recorder has been towed. Some tracks are interrupted across the divided squares, and some shortened or omitted at the focal points.

MATERIAL AND METHODS.

The material comprises 1212 specimens of young *Gadus poutassou*, ranging in size from 2.7 to 15.0 mm. in length, and all caught in March, April and May. They were collected from the standard depth of 10 metres by the plankton recorder from routes to the west and north-west of the British Isles in 1939 and between 1947 and 1955. There are eleven records from the south-west of Ireland from 1950 onwards, but only one of these is in March, and only three before mid-April. Between 1951 and 1955 seven records were secured, in March and April only, on a route extending from the mouth of the English Channel down into the Bay of Biscay.

It had been hoped that the routes used by the weatherships on passage to and from the various weather stations would have remained identical, but changes in the positions of these stations, changes in the scheme of reliefs, and occasional special requirements, have resulted in a fan of tracks, too widely separated to be approximated to "standard routes" (see Text-fig. 1). The study of the distribution on set lines had therefore to be abandoned. Of the possible alternatives, the method used by Glover (1952) for these Atlantic routes, in which the area is divided into squares, and the number of organisms per square is determined relative to the number of samples¹ in that square, appeared to be the most useful and has been adopted. The arrangement is not identical with Glover's as it was convenient to select square boundaries which approximated most nearly to the 100 fathom line, and thus reduce the number of squares to be further sub-divided to four; but the reference letters and numerals are the same, in relation to latitude and longitude, as those used by Glover. Text-fig. 1 shows the area sampled, the spread of some of the representative tracks, the boundaries of the areas used by Smed, and the squares which are sub-divided. The extent of the sampling within the squares will be indicated in the Text-figures concerned, but only a few squares, and these mostly at the margins of the area, were sparsely sampled.

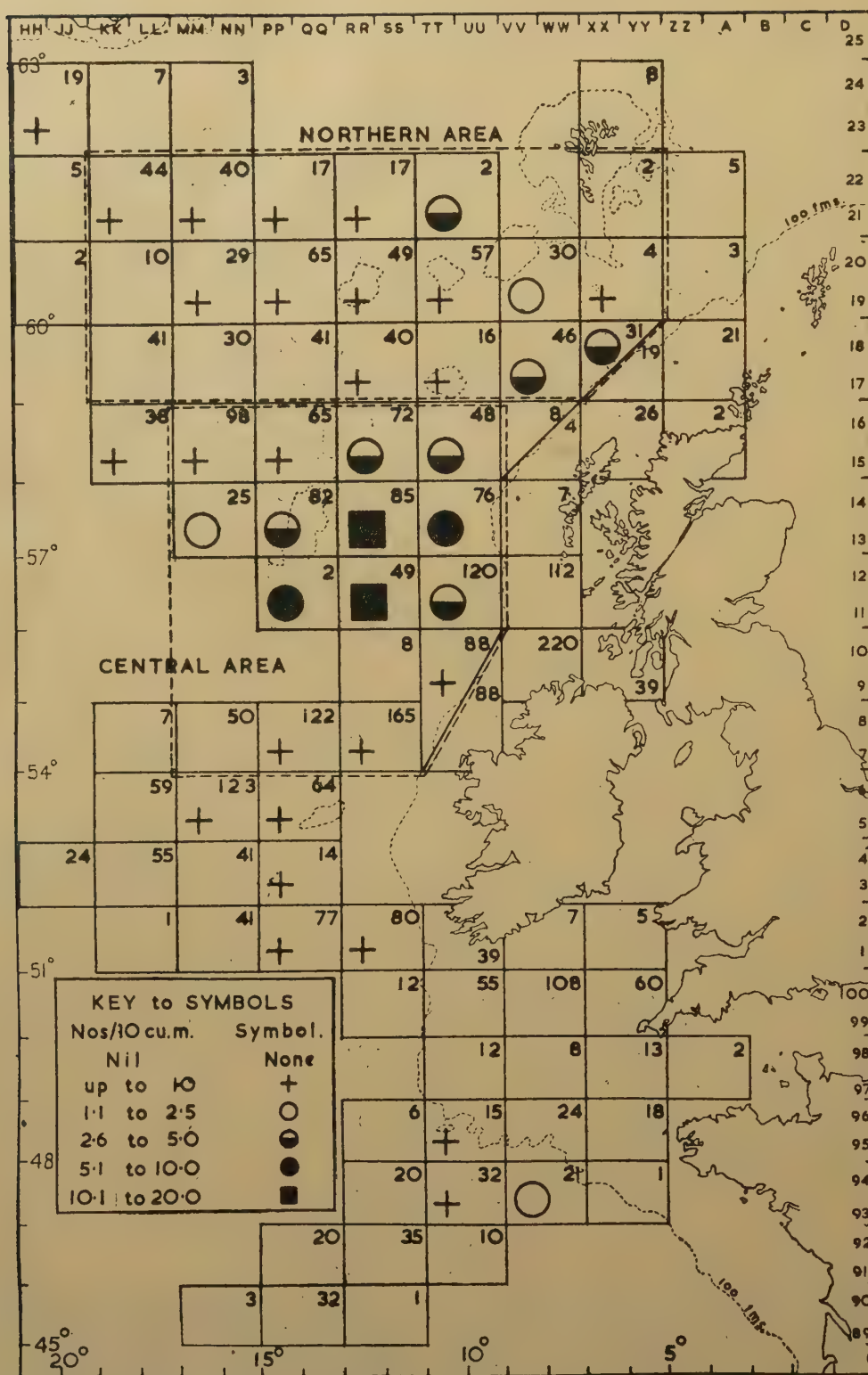
All specimens were measured, and the total length recorded. For convenience the measurements are grouped as follows: less than 3.5 mm., 3.5 to 7.5 mm., 7.5 to 12.5 mm., and over 12.5 mm. The largest did not exceed 15 mm. The results are shown grouped together to indicate the distribution of all catches over the whole period of sampling, and divided to show seasonal variations and fluctuations from year to year; and the numbers found are related to a standard 10 cu. m. sampled, as this provides a *reduction to the standard* in practically every case.

DISTRIBUTION

(i) *Range of Occurrence.*

In Text-fig. 2 the mean numbers per 10 cu.m. are shown for the squares into which the area is divided, using all the material available (taken, as already noted, from March to May inclusive, in the years 1939 and 1947 to 1955, and in no other

¹ The word "sample" is used here to connote a 10-mile block of a C.P.R. record, which has filtered approximately 3 cu. m. of water.



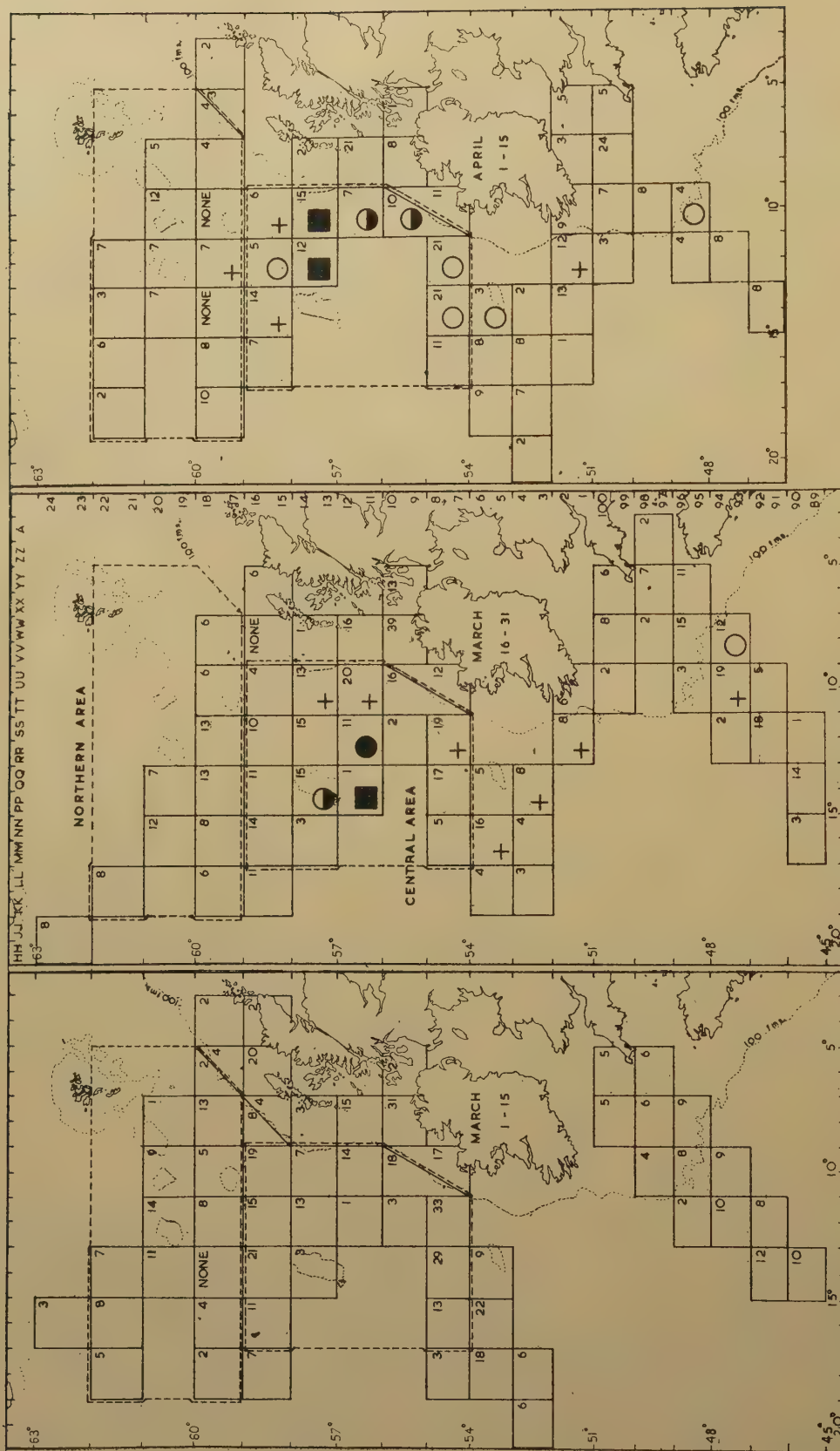
TEXT-FIG. 2.—Chart showing: (i) the mean number per 10 cu.m. per square of young *Gadus poutassou* caught in March, April and May in the years 1939 and 1947–1955. (ii) the two important areas within which the majority of the catches were taken (---). (iii) the total number of samples per square,

months). The largest numbers are found within the boundaries of two rectangles indicated by broken lines, with a smaller patch suggested off the Bay of Biscay and a few specimens south-west of Ireland. The densest concentration is contained within the rectangle bounded by the latitudes of 54° N. and 59° N., and the longitudes of 9° W. and 17° W. and this is referred to as the CENTRAL AREA.¹ To the north of this, between latitudes 59° N. and 62° N., and from 5° W. to 19° W. longitude, smaller numbers are found, spreading from the 100 fathom line in a north-westerly direction towards Iceland, and this area is termed the NORTHERN AREA. Although the areas are adjacent, their populations do not appear to be continuous, as will be seen from the seasonal distribution. By far the largest numbers, and the highest figures per unit volume, are found, mainly in April, in the CENTRAL AREA, which includes 88.0% of the individuals caught from 43.5% of the samples *outside* the 100 fathom line. In comparison the NORTHERN AREA includes only 10.25% of the individuals caught, mainly in May, from 23.0% of the samples. There can be little doubt that the CENTRAL AREA regularly contains the largest concentrations of young *Gadus poutassou*. It is less certain that this area is the main centre of *spawning*, as the developing eggs could have drifted anything up to 150 miles, presumably from further south in the light of the accepted current pattern. The possibility of a small patch off the Bay of Biscay must not be overlooked, but in comparison with the Northern and Central Areas the numbers do not appear to be very large, while only scattered occurrences are as yet recorded from the area south-west of Ireland. The main features of the distribution are evident from Text-fig. 2, in particular the complete absence of any specimens from squares within the 100 fathom line, even when adjacent squares outside the line contain large numbers. There also appears to be a gradient in numbers from the deeper water offshore where they are low, towards the 100 fathom line, where they are usually highest, but whether this is due to differences in the intensity of spawning or the concentration of spawning shoals, or results from the drift of the young in the prevailing currents, cannot be determined from the material available. The north-east limit of distribution appears to lie somewhat to the south-west of the shallowest part of the Iceland-Faeroe-Scotland ridge, although the sampling is insufficient to establish this point all the way across, as for example in square 22-21/RR-SS. The western limit appears to agree generally with that indicated by Schmidt, although few of our catches occur beyond 15° W., except in the area south of Iceland.

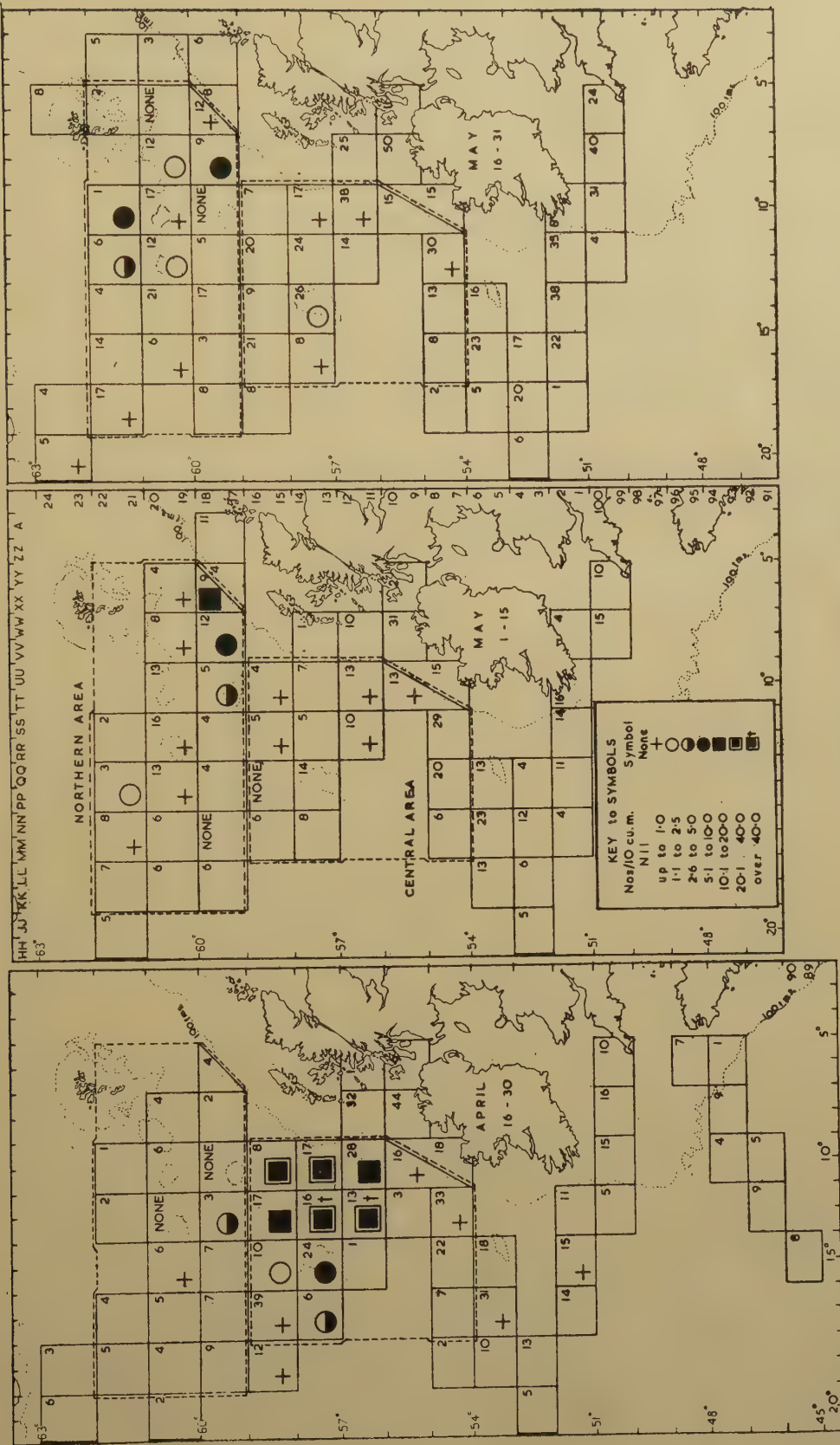
(ii) *Seasonal Distribution.*

The period during which young *Gadus poutassou* are caught by the plankton recorder at the 10 metre level is limited to March, April and May; but none have been identified on any record taken earlier than 22nd March, and the occurrences in March are limited; 1952, 62 caught; 1953 one, 1954 four and 1955 three. The

¹ Within this area the largest numbers are found between 56° and 59° N. latitude, and do not extend beyond 15° W. longitude.



TEXT-FIG. 3a.



TEXT-FIG. 3b.

TEXT-FIG. 3.—Charts showing the seasonal succession in abundance of young *Gadus poutassou* during the months of March, April and May. The months are shown divided into two, and all the results from 1947 to 1955 are included. The Northern and Central Areas are indicated by broken lines and the numbers of samples per square are shown.

majority (82.3%) were caught in April. Table I shows the distribution in time of all the catches.

TABLE I.—*Distribution in Time of Catches of Young Gadus poutassou.*

Part of month	Month.							
	March.			April.		May.		
	1-21.	22-28.	29-31.	1-15.	16-30.	1-15.	16-31.	Total.
Total caught	0	12	58	144	854	81	63	1212
% of Total	0	0.99	4.81	11.7	70.6	6.7	5.2	100

All but three of the 58 specimens caught in the last three days of March were taken on one "X" record in 1952, the remaining three were taken off south-west Ireland on one "J" record in 1955. Seven of the 12 caught between March 22nd and 28th came from the Bay of Biscay ("H" record) in 1952. The remaining five were scattered and occurred singly. The concentration of these occurrences into the last part of March, and the fact that only in 1952 were appreciable numbers taken, suggests that they are probably associated with an unusually early onset of spawning. Thus April, and particularly the second half of the month with 70% of the numbers caught, appears to be the period of maximum abundance of young *Gadus poutassou* within the area sampled.

In the above account two areas have been defined within which 98.25% of the specimens were found. These, although adjacent, have not been combined, for, as already noted, there is a difference of a month in the times of greatest abundance in each area; this may be seen in Text-fig. 3, which illustrates the seasonal distribution. The CENTRAL AREA contained large numbers in April (and the very end of March), but was sparsely populated in May, whereas the NORTHERN AREA contained only a few scattered specimens in April¹ but showed a moderate abundance in May.²

It is believed by the author that the separate identity of these two areas should be maintained for the present, at least until further data on the mode of dispersal of the sizes above 15.0 mm. can be obtained and related to the populations in the two areas. There are a number of reasons why it is believed that these two populations may well derive from successive spawnings, rather than originating at one spawning and being dispersed by drift from the original spawning area:

- (a) Schmidt (1909) had suggested a progressively later spawning time from south to north.

¹ Six individuals found in the Northern Area in square 18-17/RR-SS in April are an overlap from the Central Area in 1953 only, and are only just within the square. The boundary between the two areas was not altered to transfer these few specimens, purely as a matter of convenience in description.

² The total numbers found in the Central Area were about eight times as large as those in the Northern Area.

- (b) Hickling (1928) noted large concentrations of ripe females in March and April in a position well within the NORTHERN AREA, suggesting that there is a possible spawning concentration in this area.
- (c) The absence from both areas of specimens over 15.0 mm. appears more likely to be accounted for by Schmidt's suggestion (1905, p. 62) that the young go deeper as they grow larger than by any lack of catching power on the part of the recorder, which regularly takes Clupeidae, Ammodytidae, and other fish larger than 15.0 mm., frequently up to 40.0 mm., and sometimes up to 60.0 mm.
- (d) The size compositions of the catches in the two areas, although not identical, are nevertheless similar as may be seen in Table II.

TABLE II.—*Distribution in Time of Catches of Various Size Ranges of Young Gadus poutassou.*

Area and size range (mm.).	March.		April.				May.				All stages.	
	16-31.	%.	1-15.	16-30.	Total.	%.	1-15.	16-31.	Total.	%.	Total.	%.
NORTHERN—												
<3.5	—	—	1	1	2	28.6	4	8	12	10.2	14	11.3
3.5-7.5	—	—	1	4	5	71.4	54	29	83	71.0	88	71.0
7.5-12.5	—	—	—	—	—	—	11	7	18	15.4	18	14.5
>12.5	—	—	—	—	—	—	2	2	4	3.4	4	3.2
All sizes	—	—	2	5	7	—	71	46	117	—	124	—
Percentage.	Nil	—	1.6	4.0	5.6	—	57.3	37.1	94.4	—	—	—
CENTRAL—												
<3.5	29	44	102	184	286	29.3	3	2	5	20.0	317	29.8
3.5-7.5	33	56	34	595	629	64.0	6	11	17	68.0	679	63.7
7.5-12.5	—	—	—	60	60	6.1	1	2	3	12.0	63	5.9
>12.5	—	—	—	6	6	0.6	—	—	—	—	6	0.6
All sizes	59	—	136	845	981	—	10	15	25	—	1065	—
Percentage.	5.6	—	12.7	79.3	92.0	—	1.0	1.4	2.4	—	—	—

The smaller sizes are seen to be well represented in the catches from the Northern area, even in the second half of May, when, if this population were derived by drift from an earlier spawning in the Central Area one should expect a scarcity of the smallest sizes and a preponderance of the larger individuals. Although it would be rash to suppose that these figures prove the separate identities of the two areas, it is believed that they suggest successive spawnings rather than one in the Central Area which supplied the population to the Northern Area by drift.

In the first half of May, in the Northern Area, the catches are concentrated in the south-east corner, just outside the 100 fathom line north-west of Cape Wrath

(compare Hickling, 1928, who notes this position as producing the largest concentrations of ripe females in March and April). In the second half of the month, however, there seems to be a spreading to the north-westward, as the largest numbers are no longer found close to the 100 fathom line, although the smallest sizes are still well represented.

In each year in which the sampling has extended over a sufficient area, this same sequence of events has occurred, and there seems little doubt that it is typical of the conditions at present.

To the south-west of Ireland and in the Bay of Biscay the few specimens secured have occurred in late March and April, mainly the first half of the latter month. As already noted none have been caught earlier than March 22nd, but this may be due to the fact that only one "J" record taken south-west of Ireland has been obtained in March. This is due to the reliefs on this station via the south of Ireland usually operating from April to October or November. (In 1953 the first relief happened to be March 30th and 31st.) The route down to the Bay of Biscay, on the other hand, has operated regularly in January and February, although not in May, but again no young *Gadus poutassou* were caught earlier than March 22nd.

ANNUAL FLUCTUATIONS IN ABUNDANCE.

The numbers of young *Gadus poutassou* caught fluctuated very considerably from year to year. The lowest number caught in any one year (apart from 1939 and 1950) was 30, representing only a very small fraction (1/18) of those caught in 1955, which reached a total of 558. The sampling levels in the individual years were not, however, identical, so that this factor must be included. The most convenient way of comparing the abundance for each year is to combine the catches in the Northern and Central Areas for April and May, and relate these to the sampling within the areas. These two areas contain 98.25% of the catches and 66.5% of the samples (outside the 100 fathom line), thus providing figures which may be termed Annual Indices of Abundance; Table III shows these results.

TABLE III.—*Annual Fluctuations in Abundance of Young Gadus poutassou.*

Year.	1939.†	1948.	1949.	1950.‡	1951.	1952.	1953.	1954.	1955.	Total.	Mean.
Total number caught	(22)	102	92	(21)	30	103	48	219	552	1189	131.9
Index No./10 cu.m. (1.2)	2.15	2.05	(0.57)	0.89	1.48	1.05	5.12	15.6	—	—	6.35

† No sampling in Central Area.

‡ No sampling in Northern Area.

DISCUSSION.

As already pointed out, the young *Gadus poutassou* material taken by the recorder at the 10 metre level is complementary to that described by Schmidt (1905, 1906, 1909); his smallest specimen was one of 6 mm. length, and he described

relatively few of these small sizes ; whereas some 75% if those caught by the recorder are within 3.5 to 7.5 mm. In addition the samples were taken early enough in the year to determine the dates of capture of the smallest sizes.

The overall distribution (Text-fig. 2) does not extend the limits of the spawning areas as indicated by Schmidt (1909, fig. 13) but the concentrations found do offer some contrast with his results, as there is no evidence of *large* concentrations of young south-west of Ireland or in the north-western part of the Bay of Biscay. Our largest concentration in the Central Area (Text-fig. 2) accords with his remark (1909, p. 87) " that the quantity of the postlarval fry of the Poutassou increases greatly as we follow the 1000 metre line from Iceland and the Faeroes towards the south ", and there appears to have been little change, if any, in the position of this dominant concentration in the past 50 years. In our Northern Area (Text-fig. 2), the smaller numbers found are of the same order relative to the Central Area as was determined by him.

In the areas to the south-west of Ireland and in the north-western part of the Bay of Biscay our catches are insignificant in relation to the importance of these areas as suggested by Schmidt, although he does say that off south-west Ireland the numbers were " much smaller " (1909, p. 87). The mean number per 10 cu.m. is only 0.16 for these two areas, and is maximal, as it is based on the sampling in the only three squares in each area in which specimens were caught. In the CENTRAL AREA the mean for *all* squares is 3.07 per 10 cu.m., and in the Northern Area with several blank squares, it is 0.68 per 10 cu.m. In spite of the limited sampling in March off south-west Ireland, where there is only one record in this month (30-31 .iii. 55), the few specimens caught have all been of very recent hatching, ranging in length from 2.7 to 3.5 mm. Thus it does not seem likely that large concentrations earlier in March have been missed, or there should surely have been some of the larger stages among those caught at the end of this month and in April. This contention receives some support from the fact that in the north-western part of the Bay of Biscay no specimens have been caught earlier than March 22nd, although there was sampling in January and February. It is difficult to accept the possibility that a spawning off south-west Ireland would take place earlier than one in the Bay of Biscay, when the most northerly area of spawning—off Cape Wrath—is later than that immediately to its south. There is therefore, little evidence from the recorder material of any significant spawning since 1947 in the areas off south-west Ireland and in the north-western part of the Bay of Biscay.

The statement by Schmidt (1909, p. 114) that the principal spawning time is " spring and the end of winter ", specified on p. 85 as " February to April ", appears to hold for the results as shown by the recorder survey,¹ although as the earliest date on which a young *Gadus poutassou* was taken was March 22nd it postulates an incubation period of at least 21 days if spawning actually commences in February. This seems unlikely as the cod egg requires only 13 days at a tempera-

¹ As the recorder takes such a small sample at any one point on its track, it is possible that a very low intensity of spawning earlier than the date given might occur without being detected.

ture of 9° C., haddock 10 days, and coalfish 6 days. Travis Jenkins (1936, p. 150) refers to " . . . the general rule that in allied species the smaller the egg the shorter the incubation period ", and this suggests that at the 8° to 9° C. quoted (Schmidt, 1909, pp. 85 and 144) for the spawning of *Gadus poutassou* (the egg probably being about 1.0 mm. in diameter see p. 200), a period of 21 days would be much longer than might be expected in comparison with the other medium sized and smaller gadoids. From our material it seems unlikely that heavy spawning commenced anywhere earlier than the first half of March. Certainly it cannot have reached its height until late March or early April to the west of Scotland, as one cannot otherwise account for the very large numbers of young found here in the second half of April. Even in 1952 when large numbers were caught in this area between March 29th and 31st it is unlikely that spawning was under way before the beginning of March. In the area north-west of Cape Wrath it seems unlikely that there is any spawning until about mid-April, and according to Schmidt (1909, p. 85) it may be as late as May off Iceland. In the absence of any evidence of an earlier spawning in the area of the north-western Bay of Biscay it seems unlikely, therefore, that there is any spawning in February. In the Mediterranean the possible spawning period is given as January to May (Gualini, 1938), but no temperature or salinity figures are given.

The range of sizes taken by the recorder sampling is very limited, none larger than 15 mm. having been caught ; this and the reduction in numbers of those over 7.5 mm. were not altogether unexpected, as Schmidt (1905, p. 62) says " . . . the older stages seek the lower water layers . . . " but it allows very little scope for any suggestion of a possible growth rate. The size distribution of all specimens caught in the Central and Northern Areas is as follows :

TABLE IV.—*Total Numbers of Young Gadus poutassou of Various Size Ranges.*

Size in mm.	Numbers.
<3.5	331
3.5 to 7.5	767
7.5 to 12.5	81
>12.5	10

Undoubtedly the smallest category has suffered losses due to individual specimens being so damaged as not to be recognized, or to being so broken up that they washed through the meshes of silk. There is some evidence from the silks that this has occurred with these very tender and fragile stages. Fortunately sufficient have remained to provide descriptions and the earliest dates of capture of these very small sizes.

Three factors must be taken into account before accepting Schmidt's suggestion that the young fish larger than 15.0 mm. inhabit deeper water : evasion, drift and mortality. It is not believed that evasion can be a significant factor, as in these Atlantic waters the instrument regularly captures metamorphosed *Myctophum*

spp. in the size range 15 to 35 mm., which must be of comparable activity in evasion with similar sizes of *Gadus poutassou*. The evaluation of the drift of these young from the areas of spawning and hatching seems unlikely to be achieved from the material available, but there is some doubt as to how far this factor is involved in this case. The distribution described is a general one based on sampling over a number of years and on tracks which for any one route have fanned out considerably and which for all the routes used have covered the probable direction of drift fairly thoroughly (see Text-fig. 1). There is no evidence, from the distribution of the catches of the various size ranges, of any size gradient from place to place, which, if drift were a factor, should have been indicated by now.

The effects of natural mortality, however, can be examined in more detail, and the decrease in numbers for the various size ranges suggested for various rates of mortality. The broad assumption of a growth increment of 0.5 mm. per day (see below), with an interval of nine days from the mean of the 3.5–7.5 mm. group (5.5 mm.) to the mean of the 7.5–12.5 mm. group (10.0 mm.) and a further interval of seven days to a nominal 13.5 mm. for the over 12.5 mm. group (none larger than 15.0 mm. were caught); gives the following figures for three arbitrarily selected mortality rates :

TABLE V.—*Comparative Mortality Rates for Young Gadus poutassou.*

Size range (mm.).	Mean (mm.).	Actual Nos.	Mortality rate per day.		
			5%.	10%.	20%.
3.5–7.5	5.5	767	767	767	767
7.5–12.5	10.0	81	486	268	83
12.5–15.0	13.5	10	340	144	22

From this it would appear that a very high mortality rate must operate before the diminution in numbers of the larger sizes of individuals becomes comparable with that actually found. In the light of the known abundance of the larger size ranges in the deeper water layers it is thought that a 20% per day mortality rate is considerably higher than could be expected; but lower rates of mortality result in a considerable discrepancy between the expected and the actual numbers in the larger size ranges. This cannot, on the basis of the information at present available, be accounted for in terms of evasion and drift; but it can be explained if the larger individuals go deeper as they grow, particularly if the descent from our sampling level of 10 metres commences soon after the larvae reach a length of 7.5 mm., more and more going down as the length increases, until all have gone at 15.0 mm.

The earliest capture of the smallest specimens is March 22nd, and the largest have been caught in the second half of April. Hence there is a nominal three to four weeks from hatching to a length of 12 to 15 mm. But in the second half of April there were still many smaller than 12 mm. so the growth from hatching to 15 mm. may not take as long as four weeks. Indeed, Schmidt's finding (1909, p. 87)

of specimens 20 mm. long at the end of May off the west coast of Scotland, with hatching possibly at the end of April suggests that the growth rate may be from hatching to 20 mm. in four weeks. An increment in length of 0.5 mm. per day might be suggested as a possible rate of growth at this period. Some support for this contention may be drawn from the occurrence in the Bay of Biscay of individuals of from 60 to 70 mm. in length at an estimated age of 4 to 5 months maximum (Schmidt, 1909, p. 88).

The conditions favourable to the spawning of *Gadus poutassou* appear to be somewhat circumscribed. According to Schmidt (1909, pp. 85 and 144) the salinity must be at least 35.2 to 35.3‰, the temperature 8°–9° C., and these conditions must occur together in the surface layers over deep water outside the Continental Shelf. Thus many areas of deep water are excluded as spawning places as one or other of the remaining requirements is not fulfilled. In the area sampled there is no evidence of large numbers of fish eggs, or of particular concentrations, on these Atlantic routes outside the 100 fathom line in February, March or April. No positive contribution can be made to the problem of the depth at which spawning takes place. The spawning time does not appear to have shifted earlier in the season with the increase in temperature in the North Atlantic. Although the temperature anomalies tabulated by Smed (1947–1954) show for the months of March, April and May gains of approximately 1° C. in 1939 and in the years from 1946 to 1953 (except for 1951) when compared with those for 1903 to 1906, the spawning off the west of Scotland and north-west of Cape Wrath appears to be taking place within the time limits suggested by Schmidt. Indeed, if spawning actually occurred in February in the 1903–1906 period, it has now shifted later, as we have no evidence of spawning earlier than the first half of March. The only significant change appears to be in the intensity of spawning off south-west Ireland and in the Bay of Biscay, where with apparently increasing temperatures spawning has diminished to the point almost of insignificance. It is tempting to suggest that with the increase in temperature in the north Atlantic generally, that reached in the areas south-west of Ireland and off the Bay of Biscay at the time that the species is ripe for spawning is now too high, and that there has been some shift of the spawning stocks to the area west of Scotland. Yet this hardly seems a tenable hypothesis when it is applied to a species which is also found in the Mediterranean and is known to have ripened gonads within the period January to May (Gualini, 1938) unless it is found that the Mediterranean and Atlantic stocks exhibit racial differences.

There is no apparent connection between the tabulated temperature anomalies and the numbers caught in the years studied up to 1953, and the weather-ship temperature records for 1954 and 1955 afford no clues to any possible connection in the two best years for the young in our material.

In the area to the west of Scotland the period of maximum abundance is undoubtedly the second half of April, yet it is possible for large numbers to occur here at the end of March followed by low numbers in April. There appears, therefore,

to be a possibility that the maximum hatching may vary in time by approximately three to four weeks, but not more, as over the period 1947 to 1955 large numbers have not yet been found in May, or even to have persisted after the end of April, and no significant numbers have been found earlier than March 28th. In the area north-west of Cape Wrath the whole of the hatching would seem to be confined to May, as very few individuals have been caught in April, and so far none have been found in June, with any intensity of sampling.¹

The material obtained from the recorder survey offers reasonable support for the following suggestions :

- (a) that the diameter of the egg is probably about 1.0 mm. (see p. 200) ;
- (b) that the newly hatched *Gadus poutassou* measures between 2.7 and 3.0 mm. in length ;
- (c) that the growth from hatching at *ca.* 3.0 mm. to a length of 13.5 mm. occupies a period of about three weeks, from which a length increment of 0.5 mm. per day is suggested at this stage of development.

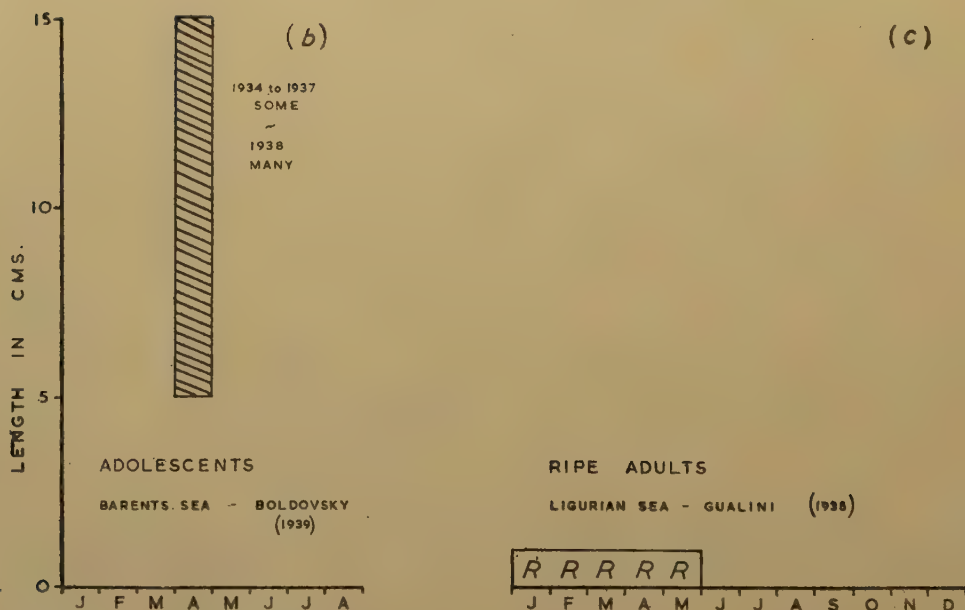
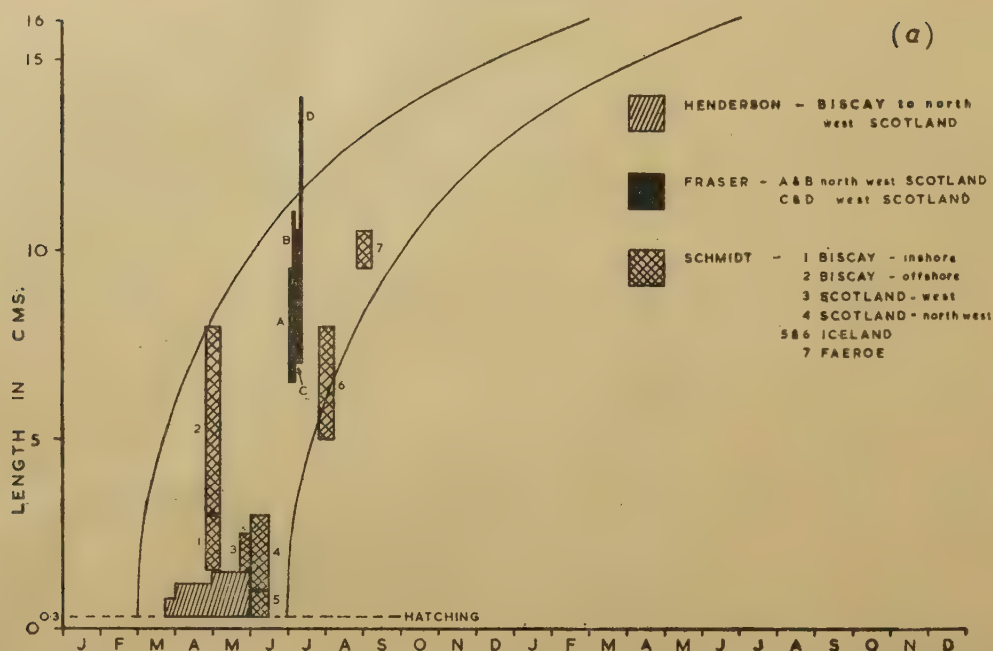
This estimate of growth rate is derived from the material collected from the CENTRAL AREA to the west of Scotland, and fits in with Schmidt's estimate (1909, p. 87) that specimens of 20 mm. in length in his material from this area were a month old (17 mm. increment in 34 days).

The recorder material, however, does not include any individuals larger than 15.0 mm., so that any assessment of the further growth rate must depend on the figures suggested by Saemundsson (1939) who gave the following lengths from his otolith studies : at 1 year—16.0 cm., at 2 years—21.0 cm., at 3 years—25.0 cm., and at 4 years—29.4 cm. It appeared profitable, therefore, to combine all the information available in the literature and from current researches to examine the growth during the first year, *i.e.* up to the nominal 16.0 cm. length quoted above.

A freehand curve of the type commonly occurring in growth rate studies was constructed from a length of 16.0 cm. to cut the time scale twelve months earlier at a length of 0.3 cm. The size ranges of samples in the various areas were examined against such a curve, the time of origin of the curve being adjusted in accordance with the apparent maximum hatching in each area. In view of the wide range of distribution and the possible succession of spawnings from south to north, coupled with the indeterminate possibilities of drift and migration (see Schmidt, 1909, p. 86), also from south to north, the figure finally drawn is a composite one, with curves drawn at the earliest and latest dates of spawning, and having the samples from all areas superimposed on the figure. Thus in Text-fig. 4 the band outlined by the two curves includes the whole period suggested by Schmidt,² and is rather longer than is demonstrated by the recorder catches of recently

¹ In 1955, for example, there were three June records in this area, on none of which were there any *Gadus poutassou*.

² Excluding February, for which there appears to be little evidence of actual spawning as no young were captured before March 22nd.



EXT-FIG. 4.—Diagrams showing (a) the occurrence of catches of larvae and post larvae of *Gadus poutassou* in the Atlantic from the Bay of Biscay to Iceland shown as histograms superimposed on the suggested growth-rate path for spawnings from March to June inclusive. (b) the occurrence of adolescents in the Barents Sea in certain years. (c) the occurrence of ripe adults in the Mediterranean.

hatched young *G. poutassou*, although these results do not sample the Icelandic waters to any extent. The catches of larger individuals are obtained mainly from Schmidt (1905, 1906, 1909), but some additional samples were provided by Dr. J. H. Fraser of the Marine Laboratory, at Aberdeen, of the Scottish Home Department. I am indebted to Dr. Fraser for the opportunity to examine and measure some collections of *Gadus poutassou* obtained in July 1955 to the west and north-west of Scotland, and for permission to use the figures in this study of the growth rate.

It must be emphasized that in the absence of sufficient data to provide for the mathematical construction of the true curve of growth rate, that shown in Text-fig. 4 must be considered as a first trial only, the value of which depends entirely on the extent to which the plotted samples of the larger size ranges fit. In general the majority of the samples fit fairly well within the limits shown by the two curves, but one group taken by Schmidt in Icelandic waters appears to extend below, and one group taken by Fraser west of Scotland appears to extend above, the levels which might be expected. There are, however, important differences in the apparatus used at various times to provide the samples plotted in Text-fig. 4, and these, coupled with divergent growth rates, may well account for the apparent discrepancies. The plankton recorder has not sampled any sizes above 15.0 mm., but has sampled down to the hatching stages at 3.0 mm. Schmidt (1905, p. 2) using a Petersen young fish trawl has caught relatively few of the sizes below 8.0 to 10.0 mm. and hardly any below 6.0 mm., while Fraser used a pelagic trawl which will have lost, seriously, the lower end of the size range although it ensured an adequate sampling of the upper end.

Two additional items are shown, on separate base lines, in Text-fig. 4: the period of occurrence of ripe adults in the Ligurian Sea (Gualini), and the catches of adolescents in the Barents Sea (Boldovsky). The first of these is not considered to be related to the spawnings outside the Straits of Gibraltar, but is indicative of a spawning period commencing not earlier than January in the warmer waters of the Mediterranean. Schmidt's speculation (1909, see p. 88) on the possibility of a spawning off the coast of Portugal earlier than that in the Bay of Biscay, perhaps as early as February, requires to be confirmed, even if racial differences between the Mediterranean and the Atlantic stocks should be discovered. Any speculation on the origin of the adolescents found in the Barents Sea in April is complicated in the extreme by the possibility of a much retarded rate of growth in these colder Arctic waters, whereby the top end of the range caught might be over one year old, although it seems unrealistic to suggest that the bottom end of the range could be, yet even these are larger than could be expected if they had originated from spawnings in the previous month. It seems equally unlikely that a possible spawning off the coast of Portugal in February (see above) could have given rise to these samples, as both growth and transportation appear to be markedly out of proportion with the time interval.

There remains, therefore, the possibility of another spawning area as yet

unknown, particularly in the light of the very wide distribution of the adults in the polar basin (Jensen, 1905), but there is at present no information on which to assess the value of this suggestion.

SYSTEMATIC NOTE ON YOUNG STAGES AND EGG.

Many of the smallest sizes of young *Gadus poutassou* are taken by the recorder, thus offering the opportunity of describing the sizes below that of 6.0 mm. at the bottom of Schmidt's (1905) size range. In all the stages described from the recorder material the eyes are fully pigmented and the notochord is straight. There are indications of interspinous regions on the caudal fin in specimens down to 5.0 mm., but none below 6.0 mm. show any indications of interspinous regions in the unpaired fins. The pectoral fins show faint indications of interspinous regions in sizes down to 4.0 mm. but below this size are no more than fan-shaped folds. The ventrals are absent. The yolk-sac appears to be relatively small, even in the smallest specimen taken, and does not always show any contents. In some there are yolk granules, but the absence of these in the other specimens may be due to damage in the recorder, in which these very fragile larvae are only too easily compressed.

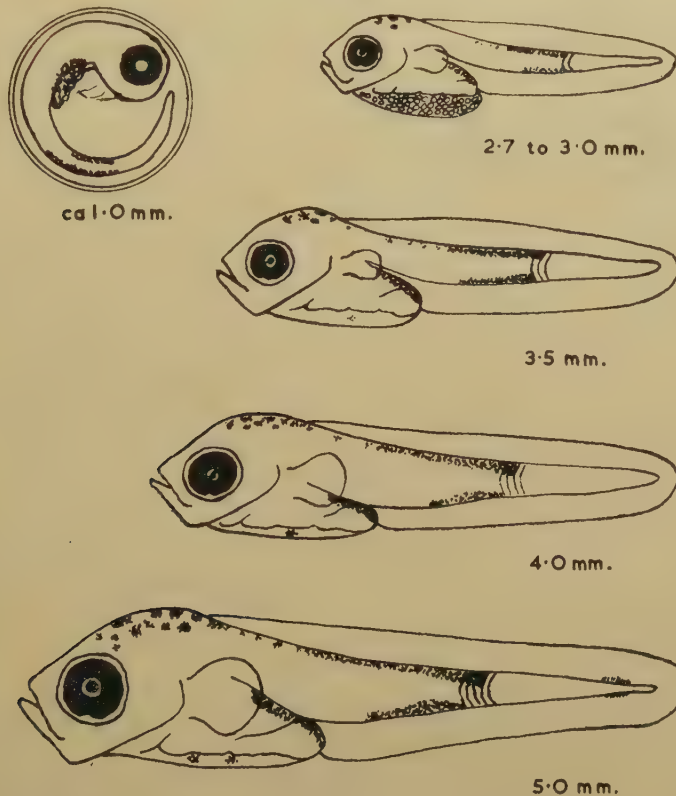
The most characteristic feature of the species, however, the larval pigmentation pattern, is readily distinguished even in the smallest individuals, although some areas of pigmentation are less extensive, or less dense, in the earliest stages than they become later on. The salient features of this pigmentation are noted here, and shown in Text-fig. 5, the sizes selected for description ranging from what appears from the recorder material to be the length at hatching of 2.7-3.0 mm. to a length of 5.0 mm. just below that of the 6.0 mm. specimen described by Schmidt (1905, p. 58).

2.7-3.0 mm.—In the few specimens available the occipital pigment is represented by four or five chromatophores only, not quite as strongly marked as in the later stages. The abdominal pigment is fully developed, consisting of many closely packed chromatophores which do not appear to develop further in density or extent in the later stages. The pre-anal pigment is not usually present, although a small faint chromatophore was seen in one specimen. The post-anal pigment bars are present and quite characteristic of the species. Both dorsal and ventral bars terminate posteriorly on the same myotome. The continuous portion of the dorsal bar does not reach a point above the posterior end of the abdominal pigment, but one or two isolated chromatophores are situated in front of the bar. The ventral bar does not extend as far forward as the dorsal, and is not continuous with the abdominal pigment in this or any of the later stages described here.

3.5 mm.—The occipital pigment is now more dense, and usually consists of six to ten chromatophores. The pre-anal pigment is limited to a single faint chromatophore, not seen in all individuals of this size. The dorsal of the two post-anal bars now extends one myotome further back than the ventral bar, and does not quite reach, anteriorly, a point above the posterior end of the abdominal pigment.

Occasionally one or two isolated chromatophores are found in front of this point.

4.0 mm.—The occipital pigment is a little more extensive than in the 3.5 mm. stage, with some indication of an extension posteriorly. There are usually one or two faint pre-anal chromatophores. The dorsal of the two post-anal bars extends two myotomes further back than the ventral, while at its anterior end it now extends just in front of a point above the posterior end of the abdominal



TEXT-FIG. 5.—Sketches showing the salient features of the pigmentation in young *Gadus poutassou* below 6 mm. The myotomes shown are exaggerated. The outline of the egg emphasizes the pigment most likely to be prominent shortly before hatching.

pigment. Some isolated chromatophores may be found between this point and the occipital pigment.

5.0 mm.—The occipital pigment is well developed and consists of many large closely placed chromatophores. The pre-anal pigment usually consists of two or three faint chromatophores only. The post-anal pigment bars are well marked, the dorsal now terminating three myotomes further back than the ventral, and extending anteriorly to a position above the mid-point of the abdominal pigment.

A few isolated chromatophores are found between this point and the posterior end of the occipital pigment.

The Egg.—The egg of this species is not described by Schmidt (1905, 1906), and Travis Jenkins (1936) confirmed that no description was then available. Gualini (1938), writing on “*The Biology of Gadus Poutassou*” in the Mediterranean, gives a diameter of 0.5 mm. for the developing egg in the ovary, but does not describe the planktonic egg. The recorder material includes many small larvae, however, and some of the smallest (mainly those between 2.7 and 3.0 mm. in length) are found coiled up as though very recently hatched. In 1955 three very small specimens were taken south-west of Ireland in March, and one west of Scotland in April. Adjacent to the smallest of these (2.7 mm.) was a broken egg capsule which measured 1.1 mm. in diameter as nearly as could be determined.

Although none of these observations provides any direct evidence on which to base a description of the egg, the presence of the egg capsule close to the smallest larva caught, coupled with the fact that the small larvae found coiled up occupy a greatest dimension of approximately 1.0 mm. suggests that the diameter of the egg may be of this order. Some further suggestions as to the salient characteristics of the egg may be drawn from the appearance of the smallest larvae, as it appears likely that the pigmentation of apparently newly hatched larvae would be evident in an egg nearing the point of hatching, so also with the eye pigment. The abdominal pigment, and the dorsal and ventral bars of the post-anal pigment are so marked in the smallest larvae seen that these surely must be noticeable in the egg. The occipital pigment, however, may not be so evident. An *impression* of the possible appearance of the egg, emphasizing the salient features as deduced here, is included in Text-fig. 5, but it must be repeated that this is not in any way confirmed from the material at present available.

SUMMARY.

The distribution of young *Gadus poutassou* taken on the plankton recorder routes in the Atlantic is described and illustrated, showing that there are two major areas of concentration of these young fish, to the west of Scotland in April, and to the north-west of the Hebrides in May. The latter is thought to be continuous with the Faroe and Iceland areas where the young are also found. Small numbers are also found south-west of Ireland and in the north-western part of the Bay of Biscay at the end of March and beginning of April, but the numbers are insignificant in comparison with the other areas.

The occurrence in time is limited to the period March 22nd to May 31st, the largest numbers being found west of Scotland in the second half of April. It appears likely that in any area there may be a variation of ± 2 weeks in the time of spawning, as in the area west of Scotland large numbers of early stages have occurred as early as March 29th and as late as April 30th.

The sizes taken by the recorder range from 2.7 mm. to 15.0 mm., larger specimens are thought to be too deep to be taken. The shoreward limits of distri-

bution are very clearcut and coincide with the 100 fathom contour. None have been taken by the recorder in waters within the 100 fathom line. The distribution illustrated for the areas to the west of Scotland and north-west of Cape Wrath is in close agreement with that outlined by Schmidt for 1903-1906, but very little spawning appears to have taken place in 1947-1955 south-west of Ireland or in the Bay of Biscay.

The possible growth rate of the species beyond the sizes caught by the recorder is examined, and the available data are related to a growth curve developed from Saemundsson's (1929) study of sizes. The majority of the data fits the suggested curve very well, but some unexpectedly large individuals were noted in the area west of Scotland. It is suggested that these may have originated further south where spawning is a little earlier. The occurrence of adolescents of from 5.0 to 15.0 cm. in April in the Barents Sea is noted, but this population does not appear to be linked with the Atlantic stock considered in this paper and it thus suggests the possibility of an undiscovered spawning area north of the Scotland-Faroe-Iceland ridge.

Some of the smallest larvae are drawn, to complete the series from hatching to the smallest figured by Schmidt (1905) at 6.0 mm. The characteristic pigment pattern is well developed even in the smallest specimen caught of 2.7 mm. A suggestion is put forward concerning the characteristics of the egg which has not yet been described.

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THE FORMS OF *RHIZOSOLENIA ALATA* BRIGHTWELL

BY

G. A. ROBINSON, M.A.

Most authors accept five forms of *Rhizosolenia alata*. Two of these, *f. curvirostris* Gran and *f. inermis* Castracane, can be satisfactorily identified by the shape of the end process, while the other three, *f. gracillima* Cleve, *f. genuina* Gran, and *f. indica* Ostenfeld, according to Hustedt (1930), can only be differentiated from each other by the diameter of the cell. In the case of *f. indica*, the cell process is stronger and appears more conspicuous because of the greater width of the cell relative to the end process in large specimens. However, this method of identification may become impracticable at the lower limits of its size range.

Various authors give size ranges for the three forms. There is general agreement about *f. gracillima* and *f. genuina*, but less so over *f. indica*, as will be seen from Table I.

TABLE I.—*Cell-diameter (in μ) of the three forms of Rhizosolenia alata Brightwell as given by various authors.*

Form.	" <i>gracillima</i> ."	" <i>genuina</i> ."	" <i>indica</i> ."
Gran, 1905 . . .	5-7	7-15	ca.48
Pavillard, 1925 . . .	—	<20	40-70
Hustedt, 1930 . . .	5-7	7-15*	20-50
Lebour, 1930 . . .	5-7	7-15	40-70
Hendey, 1937 . . .	4-7	10-20*	20-60
Cupp, 1943 . . .	4-7	7-18*	16-54
Boden, 1950 . . .	4-7	7-15*	20-60

* Termed *R. alata* by Hustedt, Hendey, Cupp and Boden, but here assumed to be synonymous with *R. alata f. genuina* of the other authors.

Hendey (1954), in a later paper, gives only three varieties of *R. alata* Brightwell. He supports the opinion of Pavillard in combining *f. genuina* and *f. gracillima*, and renames it *R. alata var. alata*. He also lists *var. indica* Ostenfeld and *var. inermis* (Castr.) Hustedt,

Cell diameter alone can never be a very satisfactory criterion of a species; there are inevitable difficulties in establishing the upper and lower limits of diameter, particularly when ranges are conterminous or overlap. Also, it is necessary to evaluate the effect of environment and geographical distribution on cell size. Lucas (1948), amongst other workers, has shown well marked differences in the size characteristics of populations of diatoms found comparatively close together.

Apart from any environmental effect which may be superimposed, the variation in cell diameter within a species, or variety, of diatom of this type is due to the method of cell division. At division, a parent cell gives rise to two daughter cells, one identical in size with the parent, and the other smaller by double the thickness of the frustule wall, since the hypotheca of the parent becomes the epitheca of one of the daughter individuals. Hence, successive cell divisions gradually lower the modal sizes of a population. This progressive reduction in size is eventually compensated by the formation of auxospores, during which process it is possible for the diatom to increase in diameter.

Evidence for the size range of a species must therefore be largely circumstantial. The limits are usually set by the analysis of size/frequency distributions in a large number of samples. However, more factual information is sometimes forthcoming from measurements made on auxospores. Drawings of auxospore development in *R. alata* are given by Wimpenny (1936) and Cupp (1948). The spore retains one parent frustule and grows a new daughter frustule, so that it is possible to measure the size increment involved in the process. A comparison of the parent and daughter cells, while they are still joined together, does at least give a minimum size-range covered by a species.

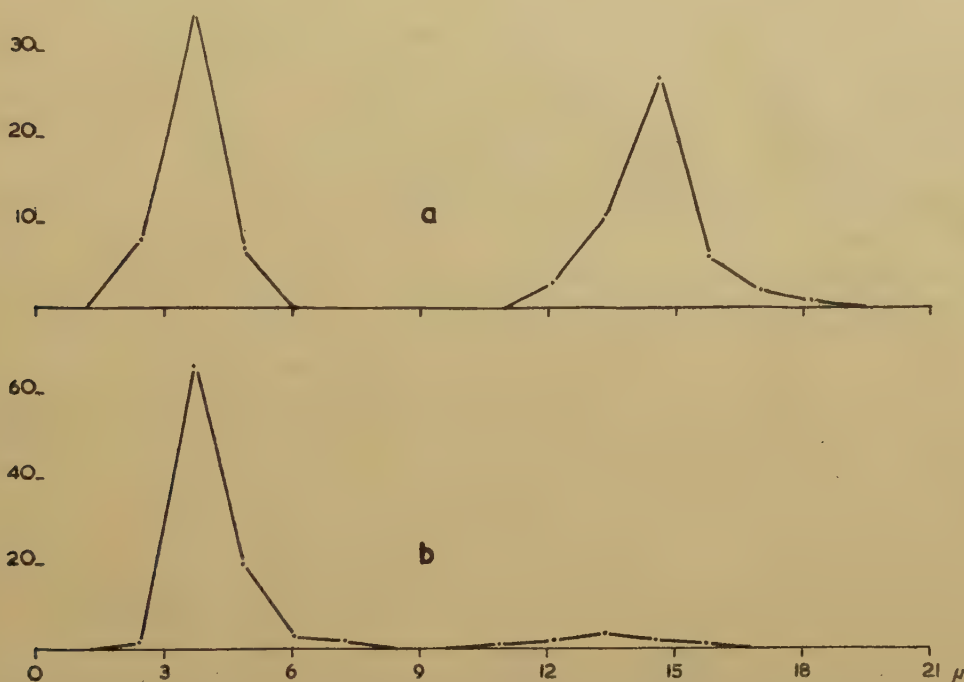
Auxospore formation covering the combined ranges given for *gracillima* and *genuina* has been described several times. Schutt (1896), working on material from the Kattegat, found auxospores giving an average change of diameter from 3.34μ to 9.35μ . Mangin (1912) found auxospores off the coast of France near Brest, which, judging from his diagram, resulted in a change in diameter from 4μ to 20μ . Wimpenny (1936) reported a change in diameter from 4μ to 16μ in material taken from the North Sea in October 1934, and Halldal (1953) found a similar change of diameter in his Norwegian Sea material of October 1948. Halldal also quotes Nordli (unpublished) as having found auxospores in the Lofoten area with an increase in diameter from 4μ to 19μ . Except for the results of Schutt, these auxospore measurements have all given size ranges which cover the conventional diameter limits of both *f. genuina* and *f. gracillima*.

Similar auxospores have been found in material collected by the Plankton Recorder. These have been measured,¹ and size-frequency measurements have been taken in a number of instances during the routine analysis of the plankton.

Fifty cells of *R. alata* forming auxospores were measured from a sample taken

¹ The measurements of all diameters were made with the aid of a micrometer in a No. 10 eyepiece, and using a 4 mm. objective, giving units approximately equal to 3.64μ . In the case of Text-figures 1a and 1b, each unit was subdivided by eye into thirds of a unit,

at $56^{\circ} 55' \text{ N. } 03^{\circ} 00' \text{ E.}$ in the North Sea in September 1953 (Text-fig. 1a) The size range of the parent generation in all cases was 2.5μ to 4.9μ , while the size of the daughter generation varied between 12.1μ and 18.2μ with 66% of the sample being 15μ in diameter. Cells forming auxospores with similar changes in cell diameter were found in samples from the same area in October 1950, October 1951 and September 1952. These clearly are of the same type as those found by the earlier workers mentioned above.



TEXT-FIG. 1.—(a) Graph showing the size-frequency of the diameter of 50 parent cells and 50 daughter cells attached to auxospores of *Rhizosolenia alata*, in a sample taken in the central North Sea. The parent cells all have diameters between 2.5μ and 4.9μ , while the daughter cells vary between 12.1μ and 18.2μ . (b) Graph showing the percentage size-frequency of the diameter of 200 vegetative cells of *Rhizosolenia alata* from the same sample.

Measurements of the diameters of 200 cells from the above sample in which auxospores were found are shown in Text-fig. 1b. The graph has two peaks, one major peak is near the lowest point of the size range given by the auxospores, and there is a smaller number with a mode at 13μ . This second peak is taken to represent the new large generation formed from the auxospores.

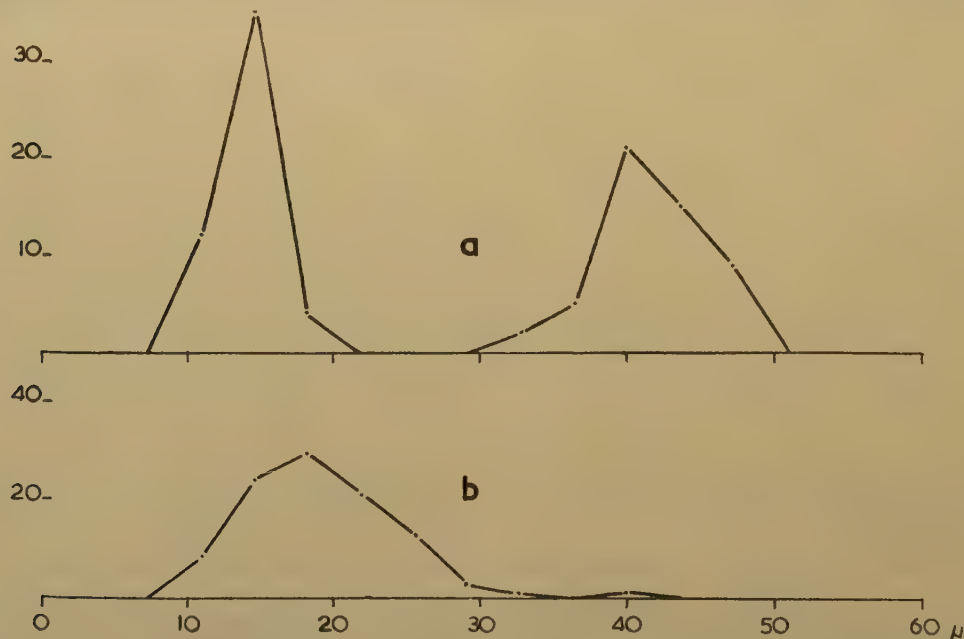
In September 1952, 5 cells forming auxospores were found in the Atlantic at $53^{\circ} 50' \text{ N. } 14^{\circ} 30' \text{ W.}$ which gave a similar size range to that found in the North Sea. The size of the smaller frustules varied between 3 and 5μ , while the size of the larger frustules varied between 13 and 16μ .

I am indebted to Dr. J. H. Fraser of the Marine Laboratory, Aberdeen, for sending me one of his phytoplankton samples containing auxospores of *R. alata*. It was taken at $59^{\circ} 45' \text{ N. } 02^{\circ} 00' \text{ W.}$ on September 7, 1954. Fifty of these were measured, and although the size of the cells forming the auxospores was the same as the previous North Sea samples, the large cells formed by the auxospores gave a slightly higher size range, with a mode at 18.5μ and the largest cell 21μ in diameter.

During August 1953, auxospores were found in the Atlantic, south-west of Ireland, which gave quite a different size range from those mentioned above. They were very scarce, and eleven samples had to be examined before fifty were measured. The parent cells were between 10.9μ and 18.2μ , with a strong predominance at 15μ , while the daughter cells varied between 32.8μ and 47.3μ , with a mode at about 42μ (Text-fig. 2a). Such auxospores have not been reported previously, and their range from about 11μ to 48μ is more of the order usually attributed to *f. indica*.

Measurements of the diameters of 200 normal cells from one of the Atlantic samples containing a few of these "larger" auxospores (Text-fig. 2b) showed a unimodal population with the diameter varying between 11μ and 33μ , with a mode at 18μ , and only one cell with a diameter of 40μ .

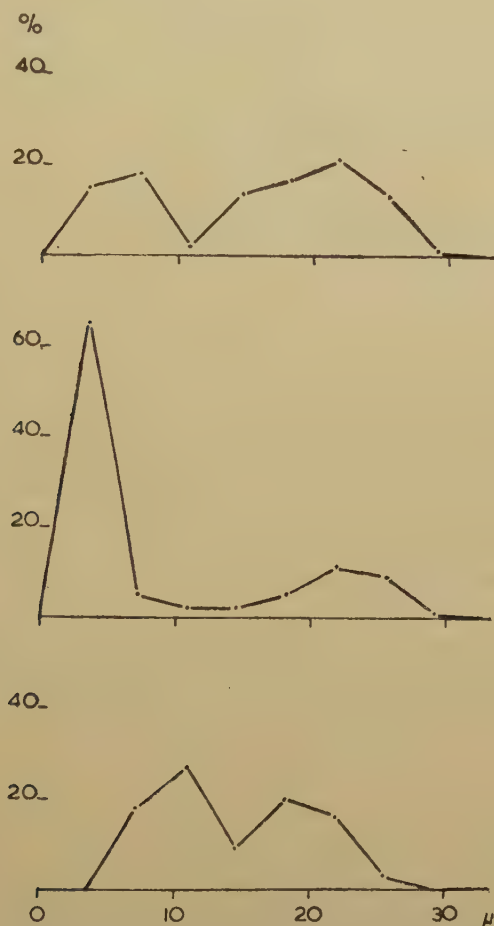
Auxospores giving two distinct size ranges have, then, been found in the Atlantic, while only one type has been found in the North Sea. Samples have been taken from the Atlantic which included cells from 3μ to 30μ in diameters;



TEXT-FIG. 2.—(a) Graph showing the size-frequency of the diameter of 50 parent cells and 50 daughter cells attached to auxospores of *Rhizosolenia alata* from samples taken in the Atlantic, south-west of Ireland. The parent cells all have diameters between 10.9μ and 18.2μ , while the daughter cells have diameters that vary between 32.8μ and 47.3μ .

(b) Graph showing size-frequency of the diameter of 200 vegetative cells of *R. alata* from a sample containing a few of the 'layer' auxospores,

examples are given in Text-fig. 3. In each case there are two modes—one which falls in the *f. gracillima/genuina* range, and the other in the *f. indica* range. Cells which can confidently be attributed to *f. indica* are not common, however, in the North Sea. Lucas (1940) reported such cells in the Recorder samples taken near the mouth of the Skaggerak in the autumn of 1937, but in the same samples, auxospores giving diameter changes of 3.5μ to 18μ have since been found.



TEXT-FIG. 3.—Graphs showing the percentage size-frequency of the diameter of 200 cells of *Rhizosolenia alata* from three samples taken in the North Atlantic.

A number of workers have observed auxospore formations by marine diatoms in laboratory cultures (see Gross, 1938). Gross himself gave measurements of parent and daughter cells from *Ditylium*, *Chaetoceros*, *Skeletonema* and *Melosira* grown in "Erdschreiber". He concluded, as a generalization, that for any species of diatom there was a limiting size above which auxospores could not be formed. Below this size auxospores were produced if or when adverse factors such as over-

crowding, shortage of nutrients, etc. became operative. It is, of course, dangerous to draw too close an analogy between the sequence of events in natural and unnatural conditions. But, nevertheless, it may be significant that all the auxospore measurements that have been reported for the smaller form give comparatively narrow limits for the diameter of the parent cell; in every case it was between 3μ and 5μ . The variation in the size of the daughter cells has, however, been greater, ranging from 9μ (Schutt) to 21μ in the present material.

If Gross's generalization that auxospores are not formed above a certain limiting size is correct, it seems unlikely that the two size ranges of auxospores were derived from the same form. If the limiting size was as large as 20μ , it would be difficult to explain why auxospores have appeared, in all cases but one, only after cells were reduced to 5μ or less. The various measurements of auxospore formation were taken at different times and places, so that it would be reasonable to expect considerable variety in the environmental conditions. Also, as the two size ranges can live together in the Atlantic, there seems little doubt that there are two forms, each with its inherent auxospore rhythm.

If, as Hustedt claims, the only criterion of difference between *f. genuina* and *f. gracillima* is cell diameter, then on the evidence provided by the auxospores, there can be no case for separating them; the minimum diameter range shown by the parent and daughter cells attached to single spores covers both ranges usually attributed to these two forms. It might, therefore, be suggested that the names *R. alata f. genuina* and *R. alata f. gracillima* be dropped in favour of *R. alata f. alata*, so following Pavillard's (1925) original contention, and the precedent more recently set by Hendey (1954).

On the other hand, there remains a case for considering *R. alata f. indica* as an independent variety covering a higher range of sizes than *f. alata* although there is considerable overlap between the two. It is hoped that further measurements on parent and daughter cells during auxospore formation will help to define these size ranges more closely.

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BULLETINS OF MARINE ECOLOGY

Bulletin No. 37 (Rees, 1957), which was issued as part of Volume V,
should have been No. 37, Volume IV.

Gummed corrections are provided:

- (above) - for the front cover,
- (below) - for the top of page 211.

The reference to Volume V inside the back cover should be deleted.

No. 37, Vol. IV.

[*Bulletins of Marine Ecology, Vol. IV, No. 37, pp. 211-246, Plates I-IV, June, 1957.*]

Volume IV will be completed by No. 38 (Rae, 1957) and by a
Title Page which will appear in 1958.



A RELATIONSHIP BETWEEN WIND, PLANKTON DISTRIBUTION AND HADDOCK BROOD STRENGTH

BY

K. M. RAE, O.B.E., B.Sc.

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INTRODUCTION.

JUST before the war, Carruthers and Hodgson (1937), and Carruthers (1937 ; 1938) drew attention to parallel trends between prevailing winds and fluctuations in catches and brood strengths of commercial fish. Later, interest in this subject was renewed when Carruthers and his colleagues presented a whole series of correlations between wind fluctuations and brood strengths which raised the possibility of forecasting recruitment to the stocks and so potential catches (Carruthers, 1950 ; Carruthers, Lawford and Veley, 1951 ; Carruthers, Lawford, Veley and Parrish, 1951 ; Veley, 1951).

The wind functions used were various ; $\sqrt{S^2 + E^2} \sim \sqrt{N^2 + W^2}$ for the haddock, $\sqrt{S^2 + W^2}$ for the herring, $\sqrt{(S - N)^2 + (W - E)^2}$ for the plaice and

$W - E$ for the hake, in each case the letter denoting the residual wind from a cardinal point over some prescribed period. Except in the case of the haddock, the forecasting technique was complicated by another variable, the month of maximum spawning. The authors postulated that this in turn was conditioned by the prevailing wind and that the relevant period for the wind function could be selected from a knowledge of the winds which had prevailed previously. Three alternatives based on the value of $\sqrt{S^2 + W^2}$ were used for the herring, three alternatives based on $N - S$ for the plaice and three based on $W - E$ for the hake.

The mechanisms behind these correlations were only tentatively suggested. In general terms, it was inferred that the surface currents induced by wind first influenced the time of arrival of the fish on their spawning grounds, or of their spawning, and then subsequently the dispersal of the eggs and fry into favourable or unfavourable environments.

Apart from stimulating much discussion, these results received criticism on two counts. Gulland (1953) drew attention to the well known pitfalls of retrospective correlation. He pointed out the inherent difficulties in establishing limits to the significance of non-linear regressions in which adjustment or selection of the variables is undertaken prior to correlation. He sought to demonstrate that, with the latitude used by the authors in selecting the wind parameters, the relationships they claimed might well be fortuitous. It is not intended here to discuss the strength of his argument as applied to the case in point; it has in part been answered by Carruthers and his colleagues (1953). The practical test of any system of forecasting can only be its accuracy over an extended period after it is evolved.

Lawford (Carruthers, Lawford and Veley, 1951) used a simple graphical method to show a relationship between wind and the survival of cod larvae. Presuming March to be the month of greatest spawning activity in the southern North Sea and the pelagic life of the fry to be about two months, he postulated that the wind blowing during March, April and May would be most relevant to their dispersal. He computed the resultant directions and mean strengths of the wind over these months in various years and charted the theoretical positions to which larvae would be carried from a central point if 1% of the wind was translated to water movement. Taking the starting point at a position which he assumed to be near the centre of a main spawning area, he showed that good year broods grouped in an area which could be identified as the great northern North Sea Eddy while the poor broods fell outside this area. Graham (1952) criticized such an interpretation of the results as being unrealistic. He argued that there was no evidence that the Ling Bank which Lawford took to be the centre of spawning was in fact more productive than other areas and that the drift of larvae "observed" by other workers did not conform to the pattern postulated by Lawford. Nevertheless, it is difficult to suppose that the orientation of broods by wind strength given by Lawford can be fortuitous. To test the hypothesis that wind and brood strength are independent, one can set up a 2×2 contingency table using the arbitrary divisions taken by Lawford (his Fig. 14).

	West wind < 4.2 m./sec.	West wind > 4.2 m./sec.	
Brood rating < 4	1	9	10
Brood rating > 4	13	0	13
	14	9	23

The odds against such a distribution occurring by chance are, therefore,

$$\frac{10! 13! 14! 9!}{23!} \cdot \frac{1}{13! 9!}$$

—or about one in a hundred thousand.

However, when thinking about the implications of these correlations and the proposed explanations behind them, two other points present some difficulty. Firstly, some of the wind functions used appear to be artificial. It is not easy to visualize the effect of any value of the function in terms of space and movement. For example, their function H which gives such excellent long-term agreement with haddock recruitment in the northern North Sea is computed from $\sqrt{S^2 + E^2} \sim \sqrt{N^2 + W^2}$. It fails to differentiate between south and east winds or between north and west winds and it is least selective near the south-west axis which is the predominant direction of the wind in these latitudes; steady south-west winds will give zero values regardless of their strength. This fact was appreciated by the authors who pointed out that, although low values of H could also arise from north-easterly winds or from weak winds of any direction, during the period of their observations they were always derived from south-west winds. Small values of H indicated, therefore, dispersal of the eggs and fry in a north-easterly direction but gave no measure of the extent of dispersal.

Secondly, the idea of planktonic larvae drifting in and out of favourable or unfavourable environments does not seem entirely satisfactory as the basis of practically all the explanations given. One can, of course, visualize the extreme case in which the larvae are wind-driven on to a beach or so far away from the place where they were spawned that temperature changes become lethal. But under more normal circumstances one might expect the eggs to be shed into a certain environment which will then change comparatively slowly. Possibly a factor more important to survival may be the type of environment into which the eggs are laid in the first place and in which they subsequently develop; that is to say, the conditions which prevail over the grounds at the time of spawning.

It was with these two thoughts in mind that the results from the Plankton Recorder Survey were searched for more direct evidence of the effect of wind on plankton distributions and so indirect evidence of changes in the environment that might be brought about by wind. The results, if not conclusive, are encouraging and have led to yet another apparent relationship between prevailing winds and recruitment to the fishable stock of haddock.

DISTRIBUTION OF *METRIDIA LUCENS*

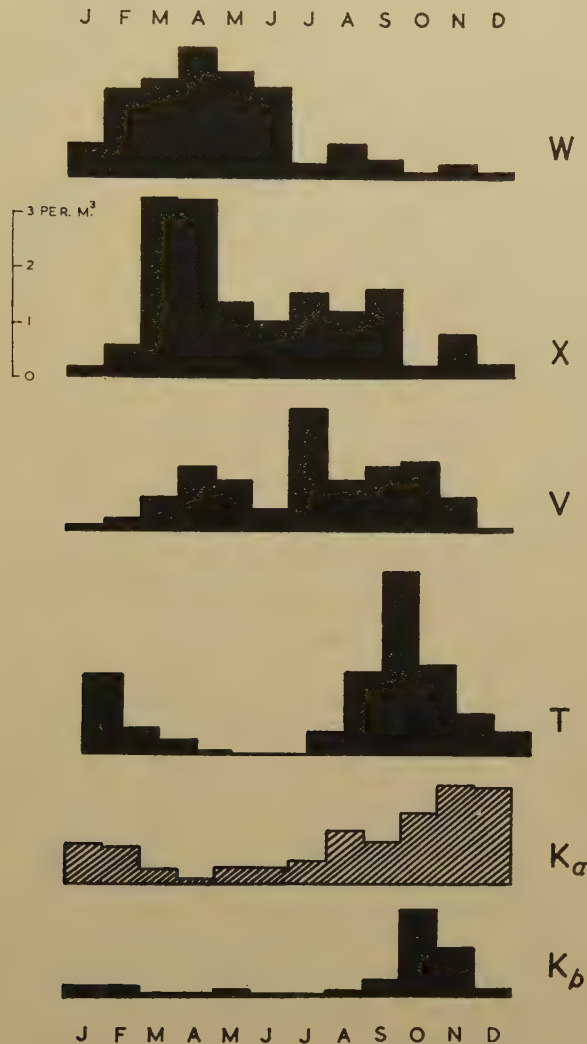
The copepod, *Metridia lucens*, was chosen as the most suitable subject for a number of reasons. If one considers the area covered by the Recorder survey, *M.*



TEXT-FIG. 1.—A chart showing those Recorder routes to which reference is made below. Each route is identified in the text by the code letter shown.

lucens is far more abundant in the open Atlantic than within the North Sea basin. Indeed, it only occurs seasonally in the recorder samples which are taken in the North Sea. It thus reflects the occurrence of a particular type of environment there.

Again, during the autumn and winter *M. lucens* has shown a fairly consistent pattern of distribution on one of the routes most frequently sampled, the K route, which runs from the Firth of Forth to the Skagerrak (see Text-fig. 1). The position of the boundary between its presence and absence can be conveniently measured along this route. There is, of course, the inherent disadvantage of using a copepod which is known to undertake pronounced diurnal migrations when all the catches



TEXT-FIG. 2.—A series of histograms showing the seasonal distribution of *Metridia lucens* on various Recorder routes, W, X, V, T and K. The positions of the routes are given in Text-fig. 1. While K_a refers to the whole length of the Forth to Skagerrak traverse, K_b only includes the first 150 miles of its length measured from the western end. In each month, all the samples obtained are averaged for the years 1949–1955 and are expressed as numbers per cubic metre of water sampled (see scale above).

are made at single depth, 10 metres below the surface, but fortunately this limitation does not affect significantly the treatment used in this study, as will be seen below (p. 253).

The overall distribution of *Metridia lucens* is not readily demonstrated from the Recorder data without resort to much detail and subsequent rationalization. In the Atlantic, the picture is complicated by two factors. Firstly, there is the effect of diurnal migration; *M. lucens* rarely occurs in appreciable numbers in Recorder samples taken during daytime and so, at 10 metres, its distribution appears more patchy than it probably is. Secondly, presumably because of some depth selection with age, very few young stages of *M. lucens* are caught by the Recorder; the situation is quite different from that found for *Calanus*, for example, in which the younger stages outnumber the adults and near adults by a plausible ratio (Rees, 1949). Moreover, it seems that *M. lucens* can complete at least three generations in the Atlantic during one year and the numbers of adults and later copepodite stages caught by the Recorder are therefore subject to rapid fluctuations. Nevertheless, there is evidence that *Metridia* has a similar succession to other indicator forms in its periods of abundance from south to north on the Atlantic routes. The monthly averages of *Metridia* on each record which have been given for the past eight years by Rae (1949-56) support such a belief.

In Text-fig. 2 all the catches taken between 1949 and 1955 in each month are pooled for the various routes. It will be seen from this smoothed representation that the species may be present throughout the year in the Atlantic on routes W, X and V but that there is a tendency for the higher averages to occur during the spring and early summer. On the K route, within the North Sea, *M. lucens* also appears to be generally present but in higher numbers in autumn and winter. However, as we will see later, the averages for the North Sea are often complicated by two centres of distribution along the length of the K route. If we take only the western half of the traverse—the first 150 miles measured from the Firth of Forth—the restriction to the autumn and winter becomes very apparent and its season becomes similar to that found on the T route in the Norwegian Sea.

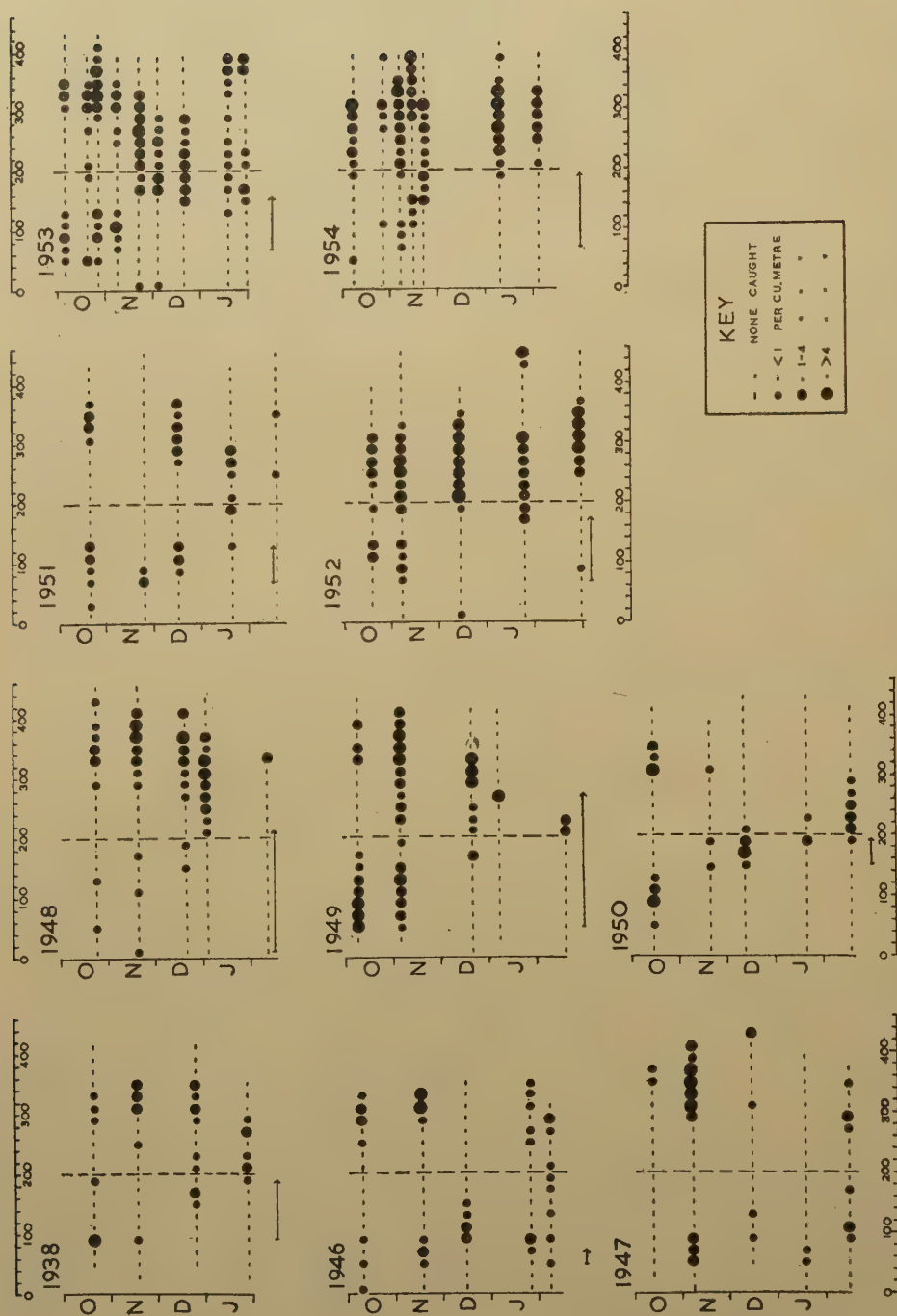
Certain caution is required in the interpretation of these histograms. As already suggested, there may be danger of an artifact due to diurnal migration of the copepods and the changing ratio of the hours of daylight and darkness with both season and latitude. For example at the northern end of the T route, there is comparatively little darkness at mid-summer or daylight at mid-winter, while this seasonal difference is far less marked in the latitude of the W and K routes. One might, therefore, seek to explain the different seasonal distribution in the two regions on the grounds that *Metridia* is known to be more abundant in the Recorder catches at 10 metres during darkness than during daylight; and doubtless this factor may play some part in accounting for its absence in the catches on the T route during mid-summer. But, to the contrary, the highest average numbers were taken on T at about the time of autumnal equinox and on X at the spring equinox and not at mid-winter when the highest proportion of samples are collected

during darkness. Also, the same difference in seasonal distribution is to be found between the W and K routes which do not differ greatly in latitude.

By the autumn of each year, appreciable numbers of *M. lucens* are caught by the Recorder in the northern North Sea. Text-fig. 3 gives a schematic picture of its distribution along the K route running between the Firth of Forth and the Skagerrak from October to January in those years for which information is available. In most years there is a tendency to bimodality in the distribution. For example, in 1946, 1947, 1949, 1950, 1951 and 1953 a western patch off the Forth appears to be quite distinct from an eastern concentration particularly at the beginning of the period. Three alternative explanations can be put forward to account for this apparent bimodality but there is no means of determining which is most likely to be correct from the data available. Firstly, as previously suggested by Rae and Rees (1947, p. 124), there may be two quite independent communities which subsequently meet and intermingle. The one on the west may mark the course of the inflowing current or drift down the coast of the British Isles while the eastern one may arise from a residual population centred in the Skagerrak or left there from the previous year's incursion. Secondly, the eastern patch may merely mark the position of the swirls and eddies which are expected to the north-east of the Dogger Bank (see Tait, 1937, his Fig. 4). It has been argued by some planktologists that free floating animals tend to accumulate in swirls, so one might conclude that in the early autumn small numbers of *Metridia* cross the western side of the route unnoticed in the inflowing current to concentrate in catchable numbers in the east. Thirdly, one might again suspect an artifact due to diurnal migration and suggest that the distributions are in reality continuous right across the traverse. Those parts of the tow sampled during the day and during the night are by no means randomly arranged along the route. The passenger ship which hauls the Recorder leaves Leith as soon after 4 p.m. as the tide permits and so the first part of the tow, the western end, is usually taken at night. The distance covered by the ship before dawn lengthens as the winter progresses while the distance steamed on the following day, during which *Metridia* are seldom to be caught at 10 metres, becomes correspondingly shorter. This is not an invariable rule because occasionally tows are made on the return trip and the timing is dictated by conditions in Copenhagen with a long steam in the Baltic and Skagerrak before the Recorder is shot.

However, whichever of these explanations or combination of them is correct, a striking feature of Text-fig. 3 is the apparent behaviour of the westernmost boundary of the distribution. With the exception of 1947, it shifts fairly regularly further offshore towards the east as the winter progresses. Both the extent and the speed of this movement vary considerably in the different years, and it is these variates which can be correlated with the prevailing wind.

It so happens that the western boundary usually falls on that part of the record which was taken during the night but this point is of little relevance. By no stretch of the imagination can it be argued that the position of the ship in relation to time of day will be conditioned on two selected voyages by a residual wind which is



TEXT-FIG. 3.—A schematic illustration of the distribution of *Metridia lucens* along the K route during the winters of 1938, 1946-54. The horizontal scale above and below each column gives the mileage from Bass Rock in the Firth of Forth, samples being taken every 20 miles along the route. In each year, the records are arranged on a vertical time scale, O for October, . . . J for January, while the numbers of *M. lucens* caught are indicated by symbols as listed in the key. The length of the arrow below each year represents the distance moved by the westernmost boundary of the distribution between the first record in November and the last record in January.

averaged over three months. So whereas errors introduced into the picture of the distribution of the plankton due to diurnal migration may weaken or obscure any correlation between the distribution and wind, such errors cannot possibly be the cause of the interaction or, indeed, introduce any systematic bias.

A RELATIONSHIP BETWEEN WIND AND THE DISTRIBUTION OF *METRIDIA*.

The months selected for correlation are November to January: the longest period over which the western patch of *Metridia* was identifiable in all ten years. The speed of apparent movement of the patch from west to east along the line is estimated by taking the distance between the westernmost edge of the patch on the earliest record in November and the latest record in January—the distance indicated by the arrow below each year in Text-fig. 3—and dividing this mileage by the number of days between the two records. It is easier to take the western boundary than the centre of distribution because the latter may be far less definite and may become confusable with the eastern concentration towards the end of the period. The wind, for the same three months, is computed from the values for the cardinal components over the northern North Sea which are based on barometric differences between three stations (Dietrich *et al.*, 1952).¹

The estimated speeds of movement are given in Table I together with the average daily wind in sea-miles per day over the three months.

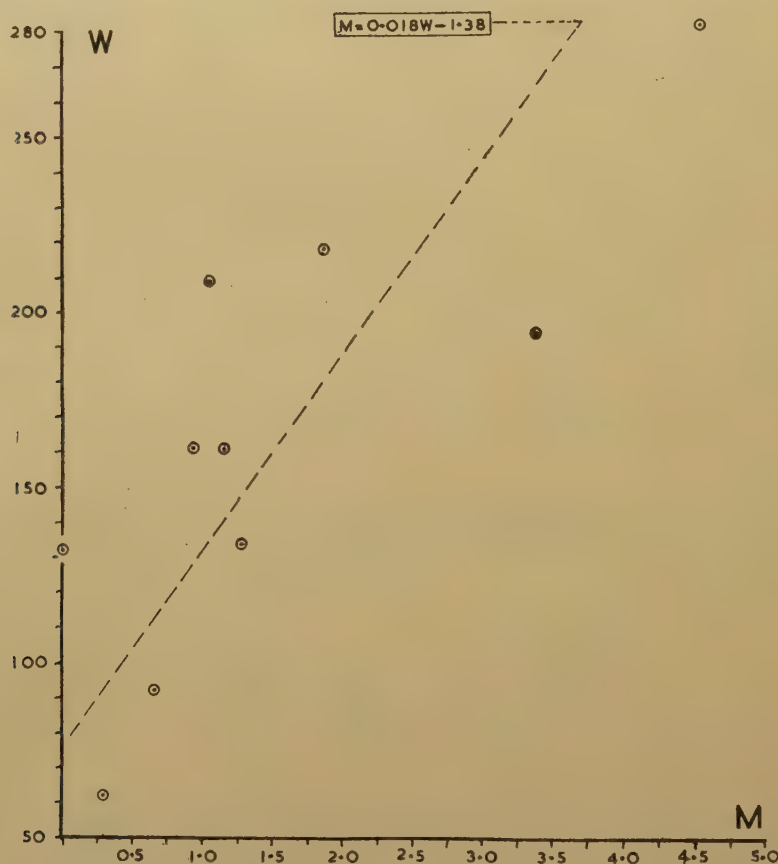
TABLE I.—*The Average Wind Strengths Over the Northern North Sea from November 1st to January 31st and the Estimated Speed of Movement of the Western Boundary of Metridia lucens on the Forth to Skagerrak Route During the Same Period, Expressed in Sea-miles per day.*

	Components of wind from		Residual wind		Component of wind from 258° true.	Easterly movement of <i>Metridia</i> .
	South.	West.	Direction.	Strength.		
1938-39	247	84	19°	261	134	1·28
1946-47	238	14	3°	238	62	0·29
1947-48	61	121	64°	136	132	0
1948-49	154	252	59°	297	281	4·55
1949-50	172	163	43°	237	194	3·38
1950-51	112	70	32°	132	92	0·65
1951-52	121	186	57°	224	209	1·05
1952-53	51	154	72°	162	161	1·28
1953-54	33	159	78°	161	161	0·94
1954-55	154	191	51°	245	218	1·88

¹ Since 1951 these German data have been kindly provided as 10-day averages, first by Dr. J. N. Carruthers through the Hydrographic Department of the Admiralty and later by Dr. J. Smed as a service of the International Council for the Exploration of the Sea.

Clearly, there is no detectable interaction between the movement of plankton and the southern component of the wind. This is to be expected as the movement is measured along a route running 78° to the east of due north. On the other hand, the speed of movement does correlate at the .05 level with the western component ($r = .7106$ with 8 d.f.) and also, regardless of the considerable variation in its direction, with the mean strength of the residual wind, $\sqrt{S^2 + W^2}$, ($r = .7160$ with 8 d.f.).

However, a much closer relationship is to be found when both wind and plankton movement are measured along the same axis; that is when we take the residual



TEXT-FIG. 4.—The easterly movement (M) of the western boundary of the distribution of *Metridia lucens* along the K route plotted against the component of the wind (W) blowing along the route. Both variates are averaged for the three months, November, December and January and are expressed in sea-miles per day. Each point represents one winter during the period 1938-39, 1946-47 to 1954-55.

carry of the wind in sea miles per day towards 78° true (see Table I). These two variates are plotted together in Text-fig. 4 and they give a correlation significant at the 0.01 level ($r = .8016$ with 8 d.f.). Assuming a straight line relationship, the

regression of the speed of movement of the plankton boundary (M) on the wind component (W) reads :

$$M = 0.018W - 1.38 \quad (1)$$

The residual error of the regression is, as one must expect, comparatively high, ± 0.90 . The available estimates of both variates lack accuracy for a number of reasons and although the errors involved do not introduce bias, they are considerable. For example, the position of the plankton at any time can only be estimated to the nearest 20-mile interval because of the method used in analysing the Recorder catches (Rae, 1952). There may be errors in charting the positions of the samples because the speed of the ship has to be measured through the water rather than over the ground. Where low numbers of *Metridia* are involved, sampling errors may also cause inaccuracies in placing the edges of the distributions. The period taken for wind never coincides exactly with the period during which the plankton movement is measured. The wind is averaged over the full three months and then compared with movements over periods ranging from 44 to 85 days, depending on the dates on which the Recorder was towed in November and January.

Although the displacement of the points is not consistent along the wind axis, a very similar relationship is found when the movement is plotted against the south-west component of the wind $\left(\sqrt{2} \cdot \frac{S+W}{2}\right)$. Then, $r = .7939$ and the linear regression reads :

$$M = 0.019W - 2.26 \quad (2)$$

Correlations can also be established between south-west wind and movement over both longer and shorter periods. No *Metridia* were found on the western half of the Recorder route in October 1947, but in the other nine years the movement and wind values computed in the same manner for the four months, October to January, give a correlation which is significant at the .05 level. A similar significance is found for the correlation between wind and movement for only two months, December and January, also taken over only nine years; no Recorder samples were available in 1946 in this case.

Although a linear regression is drawn in Text-fig. 4, and is certainly adequate for the present purpose, it appears superficially that a curve of the form $M = aW^2 - b$, or $M = aW^2 + bW - c$, might approximate better to the plotted points. For example, M correlates rather more closely with W^2 than W , giving $r = \cdot 8446$ with 8 d.f. The regression then reads :

$$M = 0.54 \times 10^{-4} W^2 - 0.13 \quad (3)$$

—and the residual error of the regression line is reduced by about 10%.

—where C represents the speed of the current 14 ft. below the surface induced by wind (W) and where B is any basic current which is independent of wind. This agrees quite well with our linear regression (1) above.

However, in more detailed consideration, there is even closer agreement between the two sets of results. Lawford and Veley concluded that above certain wind speeds a linear regression gave way either to a parabolic relationship or to another linear regression of steeper slope. The point of transition again varied between different light vessels and with different wind directions but on the average it appeared to be at about Beaufort 3 or about 250 miles per day. Such a value fits the point of curvature in Text-fig. 4 well.

A RELATIONSHIP BETWEEN WIND, PLANKTON MOVEMENT AND HADDOCK BROOD STRENGTHS.

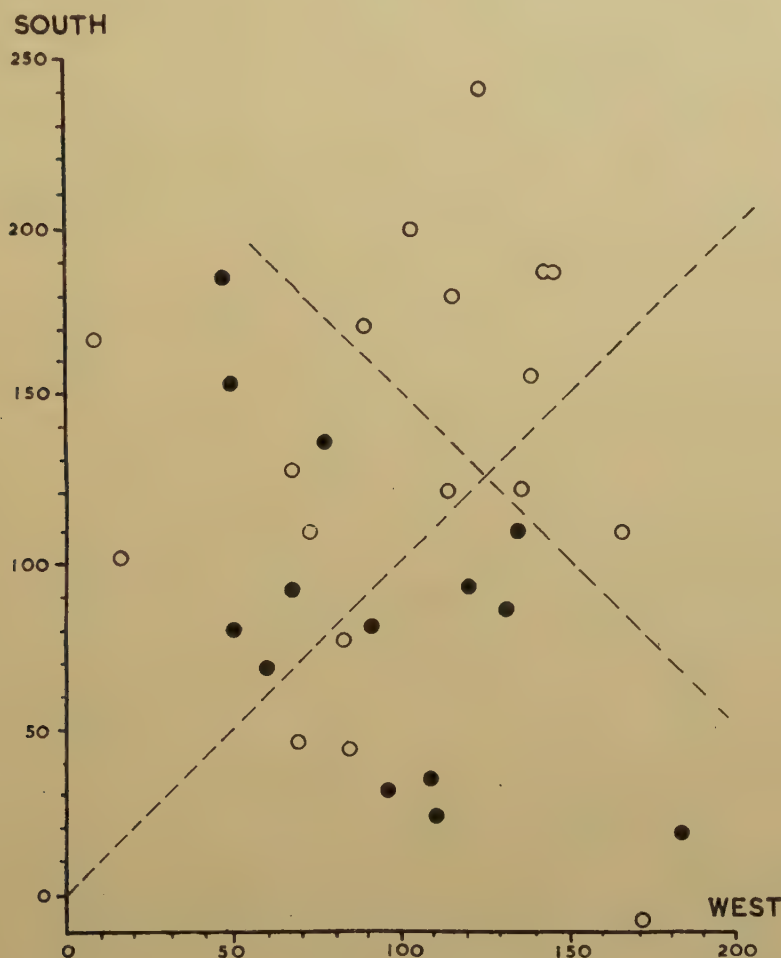
As there is good agreement between the speed of the eastward movement of the plankton and the prevailing wind, so it is possible to correlate the position of the boundary of *Metridia* along the Recorder route at a given date, the end of January, with the mean wind over the preceding months. The date of the last January record is always a few days before the 31st and as the number of days is not consistent some adjustment is necessary to provide an estimate of the position of the boundary at the end of the month. The most satisfactory method is interpolation between the positions found on the last January record and on the record immediately after it, assuming a constant rate of movement between the two dates. Clearly, this is another source of error but not a systematic one; the dates on which records are taken must be quite independent of average winds. The variation in the position of the plankton boundary at the beginning of the period in different years may also tend to weaken the correlation. The same value for wind is taken as before, the average daily strength of the component along the Recorder route during the months November to January inclusive. In Text-fig. 5, these values for the ten years, 1938 and 1946 to 1954, are plotted against the estimated position of the western boundary of *Metridia* at January 31st, measured to the nearest 20-mile unit from Bass Rock in the Firth of Forth. The correlation is significant at the .01 level ($r = .7848$ with 8 d.f.). The regression of this position (P) on wind (W) reads :

$$P = 0.87W + 35 \quad . \quad . \quad . \quad . \quad . \quad (6)$$

which, although not completely compatible with the linear regression of movement on wind (1), is reasonably close to being so. The residual variance of the regression is ± 46 .

Again, the south-west component of the wind also gives a significant correlation

Although we only have information about the distribution of the plankton for 10 years on which to establish the correlations, wind data are available over a longer period. As stated above (p. 255), the German Hydrographic Institute has



TEXT-FIG. 6.—The strength of the residual wind averaged for the months November, December and January during the winters of 1917–18 to 1937–38 and 1944–45 to 1954–55 in sea-miles per day. The black and open circles represent those winters in which the subsequent broods of haddock were above and below average respectively.

computed monthly mean resultants for the wind over various areas from barometric pressure differences (Dietrich *et al.*, 1952) and since 1950 similar data have been provided from the same and other sources.

The main spawning ground of the haddock in the North Sea is situated to the north of the line of our plankton observations and spawning takes place there between

February and May (Thompson, 1929), sometime after the date on which we can deduce the position of the plankton. Relative estimates of the brood strengths of haddock for 23 years are also available. These are based on the number of haddock between one and two years old which were caught by the Scottish research ships per hour of trawling in the North Sea. Estimates are published for the period 1918-38 and for 1945 (Raitt, 1939; Parish, 1949), while estimates for the more recent years, 1946 to 1955, have been kindly provided by Mr. B. B. Parrish and Mr. R. Jones of the Marine Laboratory, Aberdeen. Again there are many sources of error in the estimates, but the annual brood value so obtained can be taken as a rough index of the relative intensity of spawning or of the relative survival of the progeny during the first 12 months of their life, or of some combination of the two. It provides a rough assessment of the recruits to the commercial fishery in any year.

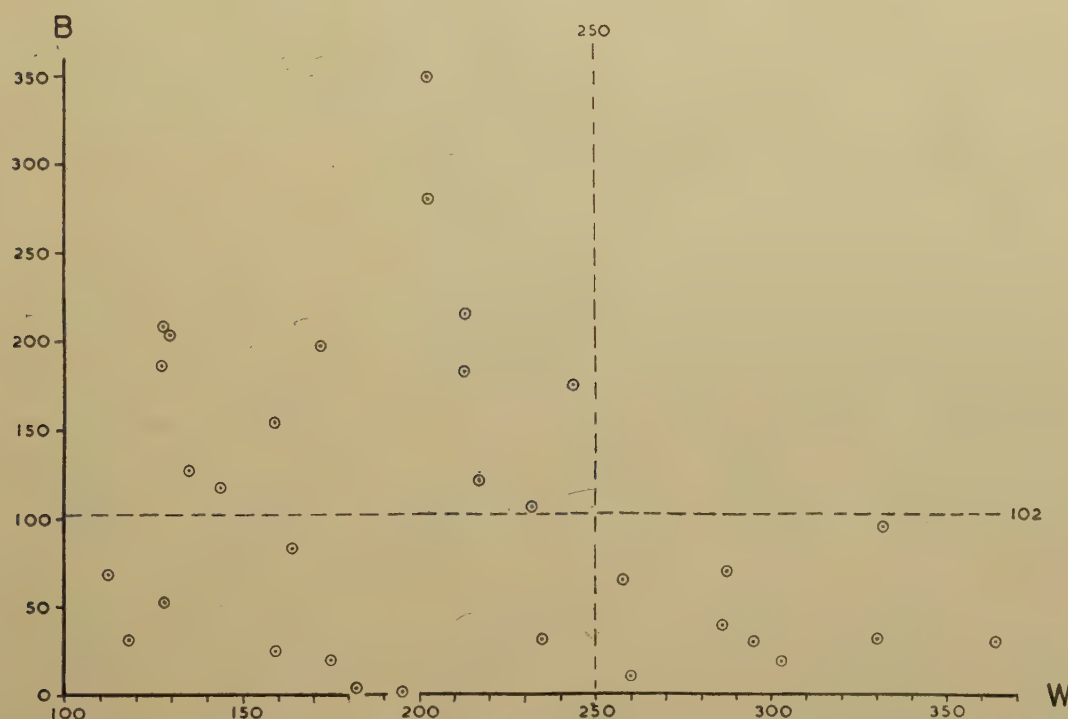
In Text-fig. 6, the approximate brood values, above and below average, are plotted against south and west wind: the position of the symbol indicating the strength and direction of the wind residual during November to January in that year. There is an obvious tendency for the better broods to group and this can be illustrated rather more conveniently in Text-fig. 7 where the broods are plotted against the south-west component of the wind residual. In each case, the average wind for the period November to January is compared with the strength of the brood spawned in the following spring; for example, the wind for the winter 1927-28 is plotted against the brood spawned between February and May 1928 which was sampled as one-year-old fish during 1929. It then becomes quite clear that the two variables are not independent of each other. All the above average broods lie over the left-hand side of the base line or are associated with the lower wind values. There is a well-defined boundary at winds of about 250 miles per day to the right of which good broods never occurred during the 32 years. With winds stronger than 250 miles per day there are 9 broods all below the average value of 102, while with winds weaker than 250 miles per day there are 9 below and 14 above average. The chances of such a distribution arising fortuitously, or that there is no interaction between wind and brood values, can be expressed by:

$$\frac{14! 18! 9! 23!}{32!} \cdot \frac{1}{14! 9! 9!}$$

which gives a probability of less than .002.

One might be tempted to postulate further that the best broods are associated with winds between 200 and 225 miles per day and that there is also falling off in brood expectancy with weaker winds. Such a view was taken earlier when the wind values were computed over a four month period, October to January, instead of the three months November to January. However, with the limited data available, it would be unrealistic to emphasize this point; there is certainly no statistical evidence here to support it.

The arithmetic means of the broods associated with winds below and above 250 miles per day are 124.8 ± 20 and 45.0 ± 8.7 respectively. But there is, overall, a predominance of lower brood values and a more rigorous comparison is not easily achieved. There is a marked difference between the distribution of values in the two categories and no transformation can be expected to normalize both. As can be seen from Text-fig. 7 the range of broods in the lower wind category spreads beyond



TEXT-FIG. 7.—The relative brood strengths of haddock (B) during the years 1918 to 1938 and 1945 to 1955 plotted against the south-west component of the wind (W) during the three months, November, December and January, preceding the spawning season. The broods are expressed in numbers of one-year-old fish caught per hour of trawling and the residual wind in sea-miles per day. The hatched lines mark the value of the average catch (or brood) and of a wind of 250 sea-miles per day.

that in the higher category in both directions and it is therefore impossible to make the respective variances independent of the means.

One cannot, of course, make the statement, which would be most useful for practical forecasting, that weak or favourable winds give good broods while strong or unfavourable winds give bad broods. One can imply no more than that winds above a critical value introduce conditions which are limiting to recruitment. So while one may forecast bad broods after unfavourable winds with some confidence,

one cannot do more than say that recruitment *may* by good in a season following favourable winds. This is to be expected. The conditions prevailing at the time of spawning can do no more than set the upper limits to the subsequent recruitment to the catchable stock some twelve months later. Whereas poor survival of fry may preclude good recruitment regardless of the number of eggs laid, the converse is by no means true. No factors can subsequently increase the potential of a really poor spawning and it may well be that the most favourable conditions will not bring the subsequent recruitment up to average. Again, the young fish face many hazards during the first year of life which may not be consistent from year to year ; so even good hatching under the most favourable conditions need not ensure better than average recruitment. The exceptionally cold winter of 1947 has already been invoked to explain the very poor survival of the brood of that year (Carruthers, Lawford, Veley and Parrish, 1951).

DISCUSSION.

We have then two premises which can be asserted with some degree of confidence. Firstly, the distribution of *M. lucens* after it has entered the North Sea in the autumn can be related to the prevailing wind. This permits a forecast to be made of its approximate distribution along the east-west axis at a date sometime before the onset of haddock spawning from a knowledge of the preceding winds. Secondly, the relative success of the haddock broods, as they can be judged by the subsequent recruitment of one-year-old haddock to the fishable stock, can also be related to the same function of the wind. Both the correlations have to some extent stood up to trial.

The correlation between wind and the movement of the *Metridia* boundary was first postulated in 1952 on the results of only 7 years.¹ Since then data from a further three winters have fitted the regression well and have enhanced the significance of the correlation.

The relationship between wind and haddock brood strength was also mooted in a slightly different form when brood values were only available up to 1948.² Estimates of recruitment during a further seven years have complied with the hypothesis and would have conformed to the forecast which might have been made. Up to 1948, the average value of the broods associated with winds of less and more than 250 miles per day were 123 and 46 respectively. Since 1948, there have been five years with winds below the critical value. Four of these have given broods above average and a mean value for the five years of 121 ; while in the only year in which the critical wind was exceeded, the brood was poor, 40.

No attempt will be made here to set up a detailed model to explain the causes behind these relationships. The object rather is to present the observations as

¹ In a paper read to the Plankton Committee at the 50th Meeting of the International Council for the Exploration of the Sea in Copenhagen, 1952.

² In a paper read to the Challenger Society at Millport, 1953. (Rep. Challenger Soc. 4 : 24-25.)

a basis for future study. However, there are one or two points which may warrant further consideration and emphasis.

First, it is important to realize that the wind has played its part before the haddock spawning season starts. Its effect on the brood must therefore be indirect and it seems reasonable to suggest that it is the orientation of certain environmental factors of importance to the survival of the larvae which is previously influenced by the wind. The relationship between wind and the distribution of *Metridia*, on the other hand, is contemporaneous. We may here deduce that the water carrying the copepods, or the type of environment which supports them, is actually orientated by the wind. The environment concerned is that complex usually associated with the incursion of Atlantic water into the North Sea being, in many respects, similar to that commonly recognized by the presence of *Sagitta elegans*.

The postulated effect of the *S. elegans* or *mixed water* environment in the Channel is well known (Kemp, 1938 ; Russell, 1939). Between 1930 and 1932 there was a lessening of the Atlantic influence in the western Channel and this was reflected in an almost complete change in the *Sagitta* taken off Plymouth ; *S. elegans* gave way to *S. setosa*, a typical North Sea form. At the same time there was a drastic reduction in the overall population of young fish taken in the plankton nets and, thereafter, there was negligible recruitment to the local stocks of herring. By the winter of 1935-36 only 20% of the herring caught were less than seven years old. Russell (1939) explained this change in terms of the food cycle. He showed a parallel reduction in available phosphates during the winter and pointed out that the phytoplankton potential and so available food for the fish fry would be limiting. However, more recent work has added a complication to this simplest and previously adequate explanation. Wilson (Wilson, 1951 ; Wilson and Armstrong, 1952 ; 1954) has demonstrated inherent biological differences between the two types of water which cannot be explained in terms of particulate food or the gross physical and chemical properties. He found that microfiltered *S. elegans* water proved conducive to the development of certain invertebrate larvae whereas microfiltered *S. setosa* water did not. There was also a suggestion from his experiments that small additions of *S. elegans* water could make good the deficiency of *S. setosa* water and some undefined growth factors must therefore be suspected. Alternatively, one is reminded of the possible effect of external metabolites postulated by Lucas (1947). Such possibilities have stimulated much interest and are now being investigated ; for example, by Johnson (1955) and Cowey (1956). However, until we have further information on the point, it might be suggested that the relationship we find between wind and haddock broods is a further example of the same phenomenon.

In the general pattern of the circulation within the northern North Sea, water from the Atlantic takes an anti-clockwise sweep, the speed and path of which is subject to considerable variation. Its direction is essentially southerly on the western side of the basin and northerly on the eastern side. The bimodal distributions of *Metridia* given in Text-fig. 3 fit such a pattern reasonably well, if one makes

the assumption that during the early autumn when the thrust is strong, the fastest moving axis of the inflow is fairly close to the Scottish coast and subsequently moves further eastwards as the thrust ebbs. Pictorially the "streams" illustrated by Tait (1937, Fig. 4) might mark successive phases in such a system. To account for the relationship between wind and plankton, it is then necessary to postulate that the direction of the flow is influenced by the prevailing wind, or that the stronger the south-west component, the more easterly the distribution of *Metridia* will become. At least such a statement would appear to be true when applied to the surface layers sampled by the Recorder. In this respect there is an interesting feature of the regressions (1) and (3) above. Regardless of whether the regression is more correctly drawn as M on W or as M on W^2 , it requires a wind of the order of 45 miles per day to give zero movement of the plankton boundary. It is tempting therefore to assume that with even weaker winds the water carrying the *Metridia* would continue in the clockwise swing it acquired in rounding the Shetlands and would spread right in to the Scottish coast. Such a consideration is, however, largely academic because wind residuals below this value rarely, if ever, occur during the winter months, as can be seen from Text-fig. 7.

Unfortunately, because of the arrangement of the Recorder routes, we only have means of measuring the distribution of *Metridia* effectively along one axis. It is not possible to assess the effect of wind on the distribution or movement of the plankton in the north-south direction. However, the fact that the best agreement between wind and movement is to be found when both are measured along the same axis would suggest that the relationship between the two is direct rather than a vector sum. It would appear more as if a body of water containing *Metridia* was being moved than a current with its own inherent direction was being deflected. Indeed, the concept of stream currents in the northern North Sea is not easy to visualize; it is difficult to explain how they acquire and maintain their identity in a water mass which, from the prevailing conditions, one would expect to be more or less homogeneous.

It may be, however, that once the *Metridia* are carried into the area they can survive in the "mixed water" which is held in the Great Northern North Sea Eddy and that it is the position of this complex which changes under the influence of the prevailing winds. Thus at various times different areas in the northern North Sea will be involved in the eddy's circulation. With strong south-west winds, the eddy will be displaced to the north or north-west and less water of Atlantic origin will cover the main spawning grounds of the North Sea haddock stocks.

One might then hazard a guess that in the northern North Sea just as in the English Channel the development of certain fish larvae is in some way dependent on beneficial properties of Atlantic water. Or, more correctly, that a deficiency of water of Atlantic origin in the environment at the time of spawning can limit the subsequent development of a brood. The evidence for such an hypothesis which is available here cannot be entirely convincing but nevertheless it does seem adequate to encourage further study with this idea in mind.

ADDENDUM.

After this account was in draft, wind data became available for the winter of 1955-56 and so there is an opportunity to test the correlations with plankton distribution over a further year.

Unfortunately, the timing of the records on the Forth to Skagerrak traverse was not entirely satisfactory; no samples were obtained during November. However, the western boundary of *Metridia* lay 70 miles from Bass Rock on October 22nd, 1955 and 130 miles from Bass Rock on February 4th, 1956. The apparent easterly movement was, therefore, 60 miles in 105 days, or 0.57 miles per day. The component of the wind along the route (towards 78°) when averaged for November, December and January was 164 miles per day. Thus the observed value $M = 0.57$ can be compared with $M = 1.57$ expected from regression (1) above while the observed $P = 130$ can be compared with the expected $P = 178$ from regression (6) above. In each case the overestimate is about equivalent to the residual error of the regressions.

However, the observed values fit the expectancy from regressions (2) and (7) above much more satisfactorily. The south-west component of the wind (towards 45°) was 132 miles per day and the expected values therefore $M = 0.25$ and $P = 125$,

SUMMARY.

1. A population of *Metridia lucens* appears to be carried into the northern North Sea in the late summer of each year. Information is available about its subsequent distribution along a Plankton Recorder route between the Firth of Forth and the Skagerrak over 10 years.

2. The speed of the apparent easterly movements of the westernmost edge of this distribution when averaged over three months (November, December and January) correlates closely with the mean residual wind blowing along the route over the same period. There remains some doubt as to whether the relationship between the movement of the plankton and wind strength is linear or curvilinear.

3. In the same way, there is also a correlation between the estimated position of the westernmost edge of the distribution at the end of January in each year with mean residual wind strength over the three previous months.

4. The same function of wind can be related to the relative brood strengths of haddock in the northern North Sea. In the 32 years for which data are available, above average broods have not occurred during the nine years in which the wind averaged more than 250 miles per day; whereas 14 above average and nine below average broods have been associated with mean winds below this value.

5. Some possible implications of these observations are discussed.

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